





FRONTISPIECE.—Carrie Bow Cay reef complex, aerial photo mosaic, March 1976.

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The Atlantic Barrier Reef  
Ecosystem at Carrie Bow Cay, Belize, I  
STRUCTURE AND COMMUNITIES

*Klaus Rützler  
and Ian G. Macintyre*

EDITORS

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## ABSTRACT

Rützler, Klaus, and Ian G. Macintyre, editors. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I: Structure and Communities. *Smithsonian Contributions to the Marine Sciences*, number 12, 539 pages, frontispiece, 232 figures, 5 plates, 47 tables, 1982.—The results of the first series of multidisciplinary investigations of the Caribbean barrier reef complex near Carrie Bow Cay, Belize, are reported in 34 papers in this volume, which begins with a summary of past work on the Belizean reefs and cays. The first section treats the structure of barrier reef habitats in the vicinity of Carrie Bow Cay, influential physical parameters such as tides and currents, geological and sedimentological history of lagoon, reef, and island substrates, and the island's environment, including its climate and the effects of hurricanes. Subsequent papers analyze the distribution of endolithic microorganisms in carbonate substrates, and the diversity, standing crop, and production in selected lagoon and back-reef habitats. Related contributions report on the benthos of an unusual submarine cave and on the surface zooplankton over reef and lagoon bottoms. One section is devoted to the systematics and local distribution of flora and fauna. Marine plants covered are plankton diatoms, benthic algae—including a detailed study of the red alga *Polysiphonia*—and sea grasses. Faunistic studies focus on hydroids, medusae, stony corals, octocorals, sipunculans, anthurid isopods, pycnogonids, a marine chironomid, ophiuroids, and crinoids. In the papers on *Polysiphonia*, hydroids, stony corals, and anthurids, all species are illustrated for identification by nonspecialists; figures of important or unusual examples are shown in the other systematic contributions. New species are described among anthurids, pycnogonids, and ophiuroids. A section on ecological responses discusses the reaction of algae to grazing pressure, the life history of an ichthyo-parasitic hydroid, the growth response of the reef coral *Montastrea annularis* to a light gradient, and associations between zoanthids and their sponge hosts. Included in this section are discussions of the ecology of the zoanthid *Isaurus duchassaingi*, settlement behavior and development of the bivalve *Malleus candeanus*, and behavioral ecology of two closely related reef fishes, genus *Acanthemblemaria*. The volume concludes with two general surveys of the barrier reef and cays, which discuss the Carrie Bow reef section and cay in relation to the overall barrier reef complex.

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## Dedication

This volume is dedicated to the 50th anniversary  
of the Great Barrier Reef Expedition 1928–1929,  
which pioneered the integration of many science disciplines  
for the better understanding of the coral reef system

## Foreword

Museum scientists tend to be specialists in a particular discipline and to work alone. Those of us, however, who study living organisms learn sooner or later that we cannot hope to understand our animals and plants fully without some knowledge of the environment in which they exist. We also learn at some point to appreciate the benefits of collaborating with fellow scientists whose disciplinary focus may differ from ours, but whose interests are related to our own through the "environmental" link. That is to say, a great natural ecosystem such as the tropical coral reef draws together researchers of many diverse disciplines.

The project "Investigations of Marine Shallow-Water Ecosystems" (IMSWE) off Carrie Bow Cay has done this very thing for many of us at the Smithsonian Institution and elsewhere, and thus we have learned far more about our organisms and their environment than we might have done otherwise. As a result, we are more than enthusiastic about IMSWE's progress. We started with only a few investigators, but as the years have passed we have grown into a multidisciplinary contingent.

Needless to say, part of IMSWE's success stems from the efforts of the principal investigator, Klaus Rützler. He is responsible for the organizing, scheduling, coordinating, and orchestrating. He has done all this with good humor and energy.

Of course, such an effort would not have been possible without the support and encouragement of the Belizeans themselves. They love their barrier reef and have high regard for its economic, recreational, and aesthetic value. Recognizing the need for understanding and protecting this precious resource, Belizean officials have approved and assisted our various endeavors since IMSWE's modest beginnings. In particular, Winston Miller, Fisheries Officer, has helped us in every way, as have members of the staff at the Ministry of Trade and Industry (after 1979 the Ministry of Health, Housing, and Cooperatives), and the Ministry of Finance.

We all know that research cannot go forward without adequate funding. The Exxon Corporation has provided part of our support, and has done it in a most generous fashion, allowing the scientists to go about their studies independently.

This volume thus represents the culmination of research effort and support from many quarters. It is the first of an open report series and serves as the basis for future contributions. It not only "sets the scene" by determining terminology and summarizing our knowledge to date, but it also points out the gaps yet to be closed. We look forward to the next decade.

September 1980

Porter M. Kier, Director (1970-1979)  
National Museum of Natural History  
Smithsonian Institution

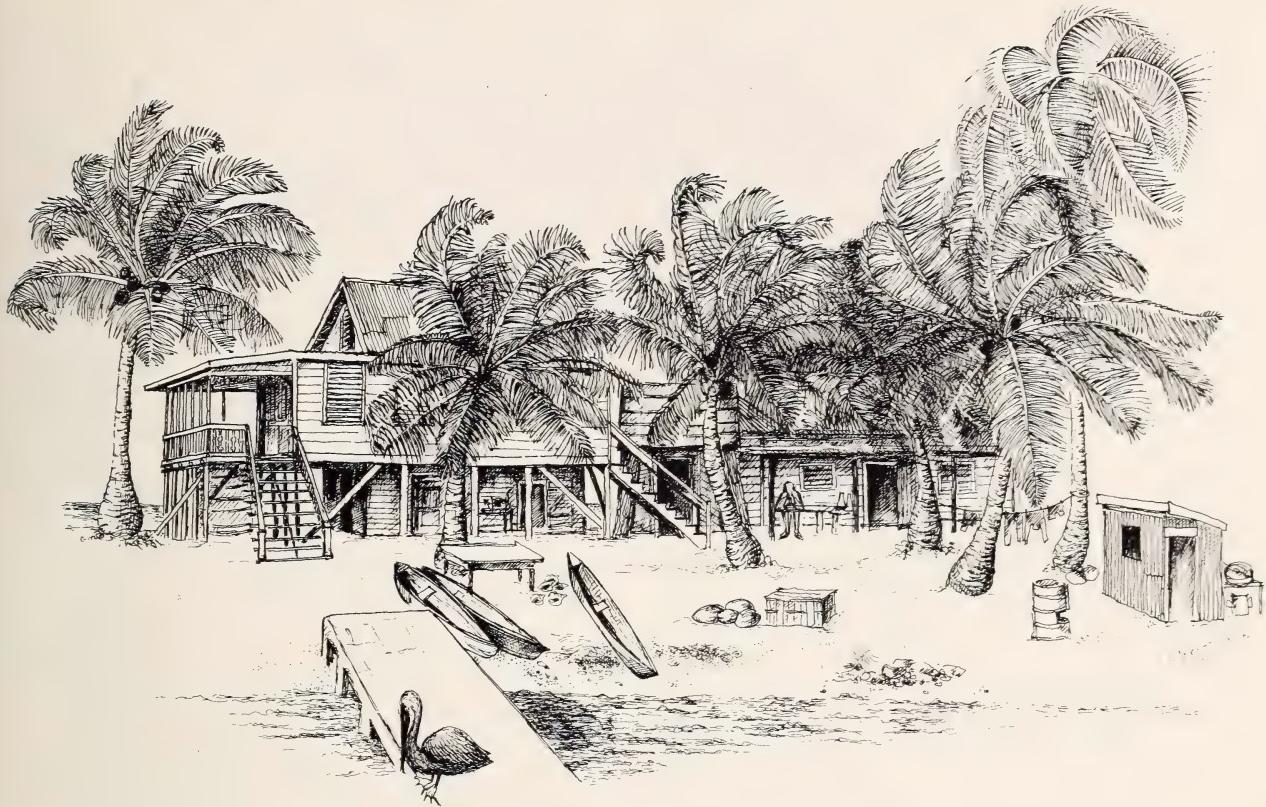
## Preface

On a windy, overcast morning of February 1972, we discovered Carrie Bow Cay. Arnfried Antonius and I (K.R.) were on our way from Stann Creek (now Dangriga) to Glover's Reef, looking for the Tobacco Cay passage through the barrier reef. We could already hear the waves pounding the coral crest but neither of two islands in front of us matched our memory of Tobacco Cay, and the crew of the charter boat from Belize City, unfamiliar with southern waters, was uncertain too. The smaller but nearer one of the cays had buildings and a solid dock so we decided to have a closer look. Minutes later we tied up to the concrete pier and walked toward the stately main building. No one was around, except for a few mildly disturbed pelicans, but a weathered sign above the gate to the main porch said "Welcome to Carrie Bow Island." On that memorable day when we first walked around Carrie Bow—a speck of sand covered by about 80 coconut trees overlooking three cottages, two outhouses, and three water tanks—we could not have predicted the developments of the eight years to come. Despite its small size, this island has been the site of a simple but functional laboratory to which more than 70 scientists from 30 institutions have come to study the well-developed reef complex nearby.

Records indicate that up to 1927 Carrie Bow Cay, then known as Ellen Caye or Bird Caye, was an uninhabited sanctuary for migrating birds and for sea turtles coming there to lay their eggs. The surrounding reef "abounded with conch, lobster, turtles, and parrot fish, all of which have been depleted by extensive trade in these commodities," according to the historical account of Henry T. A. Bowman, current owner of Carrie Bow Cay. Mr. Bowman bought the island in 1943 and decided to name it after his wife Carrie. "At that time the cay was about twice the size it is now, and was surrounded by mangrove, and had about 75 coconut trees that were planted in the early 1900's. The mangrove, breeding spot for mosquitos, was cleared off in 1944 when [he] decided to build a summer home. Of the original coconut trees only six remain today." Mr. Bowman's account also cites the stresses introduced by countless storms and hurricanes, which were particularly harsh during the past three decades but whose damage Carrie Bow Cay and the reef have managed to survive.

Notwithstanding these changes, the area remains relatively undisturbed by scientific standards, and thus is an ideal location for an ecological study of coral reefs. More significant, it is a segment of an enormous reef complex that is reasonably accessible from major cities on the North American mainland.

This volume presents the first extensive scientific account of the barrier reef around Carrie Bow Cay, Belize. It is an outgrowth of the Smithsonian Institution Program "Investigations of Marine Shallow-Water Ecosystems" (IMSWE), which began in 1970 under the guidance of W. H. Adey, A. L.

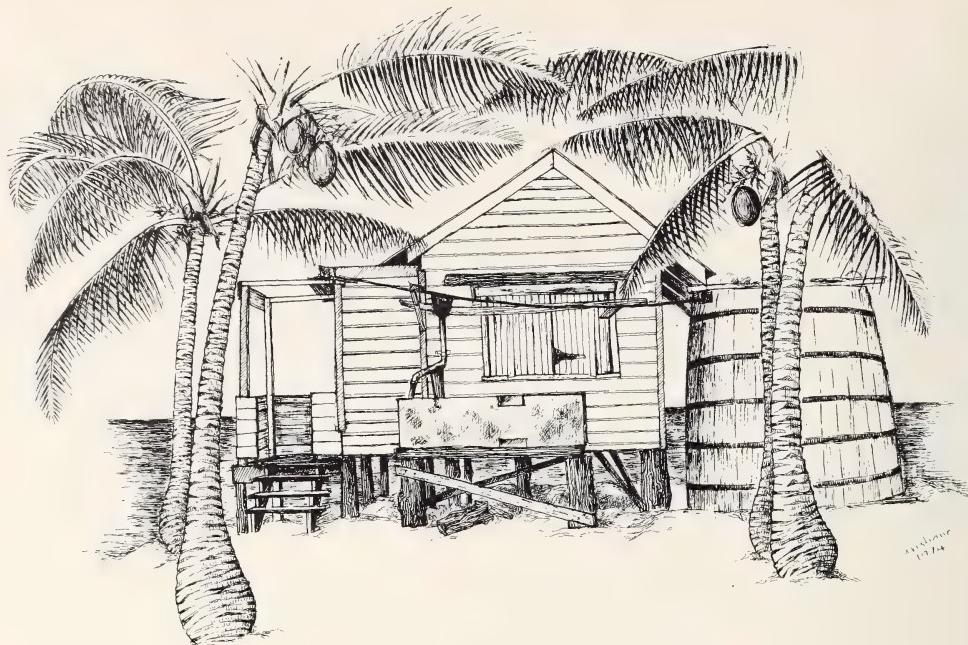


Dahl, and the editors of this volume. It was our goal to introduce long-term cooperation and a truly interdisciplinary approach to the ecological study of coral reefs and related tropical environments. Our search for a study site that would be satisfactory to the special requirements of various disciplines led us to the reef off Belize.

IMSWE evolved alongside a larger proposed project for the study of a coral-reef ecosystem that was to be a multi-institutional and multi-national program sponsored by the International Decade of Ocean Exploration. Glover's Reef atoll was contemplated as a site for that program's comparative studies and Carrie Bow Cay—although not yet seen by any of the planning committee—was discussed as an additional possibility because of its logistical advantages, particularly its location half way between the mainland of Belize and the atoll. Although the large program was not funded, Smithsonian Institution scientists carried forward the idea for an interdisciplinary study of a coral reef ecosystem.

Since that time, many enthusiasts have joined in IMSWE's collaborative investigations. Because of the growing body of information resulting from our work, we are now able to present this volume, whose purpose is to give a general introduction to the topography, oceanography, geology, and biology of the Belizean barrier reef complex near Carrie Bow Cay.

Some new terms have been introduced in this volume to describe the physiographic characteristics and zonation of the reef in this area. It is hoped



that even if these terms are revised at a later date, they will serve as an important reference for future research reports. This contribution also opens a publication series that makes it possible to add information on this reef complex as it becomes available and to keep the results in focus for subsequent additions and for a later synthesizing monograph.

The use of brand names in this publication is for descriptive purposes only and does not constitute endorsement by the Smithsonian Institution.

**ACKNOWLEDGMENTS.**—Our program and the production of this volume has received, over the years, help and encouragement from so many supporters in direct and indirect ways that it is impossible to give a just account of them all. Those who have contributed specifically to papers published in the following pages are acknowledged in the article introductions. Here, we wish to highlight the accomplishments of individuals and groups whose efforts have made our program successful and therefore made possible the production of this publication.

The Exxon Corporation extended grant support to us over the past five years; we are grateful not only for the financial aid but also for the personal interest in our studies shown by R. E. Chandler and E. W. Markowski, Public Affairs Department. Other funds came from the Smithsonian Environmental Sciences Program, National Museum of Natural History, Research Award Program and Fluid Research Fund, for which we thank D. Challinor, P. M. Kier, J. F. Mello, and S. D. Ripley. Special donations from AMOCO, Cities Service, Getty, Gulf, and Union Oil companies, and from K. Sandved and L. Taylor made possible the printing of the color plates in this volume.

The people of Belize greatly enriched our days in the field, and its



government officials helped us in many ways. W. Miller, Fisheries Officer and our scientific sponsor, patiently helped with certifications and permits. The Ministry of Trade and Industry (after 1979 the Ministry of Health, Housing, and Cooperatives) sanctioned our work, the Ministry of Finance granted exemption of scientific equipment from duty. H.T.A. Bowman ("Sir Henry") and Mrs. Bowman were our generous hosts for the past eight years. At the same time, H.T.A. Bowman, Jr. ("Junior") worked hard as our agent and guide, assisted by his wife Alice, sister Norma, and by other members of his family. H.T.A. Bowman III ("Henry") has read the tide gauge installed by us at Pelican Beach Motel, Dangriga, for the past four years.

For many years the single most important person for the program was M. R. Carpenter, who solved logistical problems at home and in the field. Mike was preceded, or at times relieved, as field manager by H. Adolfi, A. Antonius, R. J. Larson, A. B. Rath, R. H. Sims, and B. Spracklin. Others who contributed to our comfort on the cay include people known familiarly to us as Frank and Japs, staff members of Pelican Beach Motel, and Emily, Ernie, and Genevieve, our cooks. Invaluable logistical help was also provided by C. Moore of Sen & Co., Belize City. At the National Museum of Natural History our study benefited greatly from the administrative expertise of C. A. Ossola, M. Parrish, and M. R. Tanner and from the technical assistance of C. G. Ahearn, W. T. Boykins, A. C. Cohen, L. G. Cole, R. J. and K. S. Larson, and K. B. Sandved. J. Petroski, Travel Services Office, did miracles with airplane reservations.

This volume is the product of our collaboration with a number of patient authors and several dedicated assistants and goodwilled advisors. Presentation was shaped at an early stage by the skillful editing of V. V. Macintyre and the proficient illustrating of I. F. Jewett. M. Parrish and A. Stonework typed or retyped most of the contributions. S. D. Cairns, M. R. Carpenter, M. Parrish, and D. S. Robertson helped as editorial assistants. C. Schöpfer-Sterrer created the accompanying ink sketches and G. J. Thomas took the aerial photographs for the frontispiece. The following colleagues helped us as reviewers or scientific advisors: W. H. Adey, F. M. Bayer, T. E. Bowman, M.

A. Buzas, S. D. Cairns, D. R. Calder, F. A. Chace, B. B. Collette, M. E. Downey, G. L. Hessler, R. S. Houbrick, E. Kirsteuer, C. G. Messing, J. N. Norris, D. L. Pawson, H. Pulpan, J. Rosewater, and T. Waller. Finally, special thanks are due to A. L. Ruffin, managing editor, B. J. Spann, editor, and L. J. Long, production manager, of the Smithsonian Institution Press, for seeing this publication through the final stages of production.

# The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I

## Introduction

*Klaus Rützler  
and Ian G. Macintyre*

The barrier reef off Belize, Central America, has received the concentrated attention of scientists only within the past two decades. Interest in this area dates back to the late nineteenth century, however, the first scientific reference to the Belizean reefs having been made by Charles Darwin, himself, in an 1842 work, *The Structure and Distribution of Coral Reefs* (pages 201–202). Using information provided by Captain B. Allen, Darwin discussed the bathymetry associated with Belizean reefs and included them in his classification of principal reef types.

Early studies of the natural history of Belize, then known as British Honduras, focused not on the reefs but on incidental collections taken along the shore or by dredge hauls by residents of the colony and by visiting individuals and expeditions, most notably the “Pawnee” (1925) and “Rosaura” (1937–1938) expeditions. One of the oldest such records is the description of a new sponge, collected near Belize (now Belize City) by Priest (1881). Other systematic work on early collections dealt with algae (Taylor, 1935), sea-grass *Thalassia* (den Hartog, 1970), sponges (Burton, 1954), cnidarians (Boone, 1928a), crusta-

ceans (Boone, 1927), mollusks (Boone, 1928b; Marcus and Marcus, 1962; Robertson, 1975), echinoderms (Boone, 1928c; John and Clark, 1954), and fishes (Breder, 1927; Tucker, 1954; Robins and Starck, 1965; Birdsong and Emery, 1968). In addition, studies relating to commercial fisheries were reported by Smith (1939, 1941) and Craig (1966).

The first investigations focusing on the cays and reefs of Belize were undertaken by the “Cambridge Expedition to British Honduras” (1959–1960) led by J. E. Thorpe (Thorpe and Stoddart, 1962). Some members of the expedition mapped 40 cays, including Carrie Bow Cay, and collected samples of their flora. They also discussed the origin, formation, and distribution of reef and mangrove cays, and showed the migration of some of these cays on the basis of exposed beach rock (Stoddart, 1960). Another expedition team mapped bottom characteristics and identified coral species from around Rendezvous Cay, and conducted experiments on coral behavior in response to external stimuli (Thorpe and Bregazzi, 1960). Subsequently Stoddart, one of this expedition’s participants, surveyed in detail the biology and geology of the Belizean atolls, that is, Turneffe Islands, Lighthouse Reef, and Glover’s Reef (Stoddart, 1962a). At this time he also initiated an interesting series of studies concerning

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the hurricane destruction and post-storm recovery of cays and coral reefs (Stoddart, 1962b, 1963, 1969, 1974).

A second stage of intensive research activity was spearheaded by E. G. Purdy of Rice University, under whom several major projects—for the most part doctoral dissertations—treating various geological aspects of the barrier reef complex were completed between 1961 and 1967. Most of this work appeared in a volume edited by Wantland and Pusey (1975) that focused on sediments and processes of sedimentation and diagenesis (L. R. High, Jr., pages 53–96; M. R. Scott, pages 97–130; W. C. Pusey III; pages 131–233; W. J. Ebanks, Jr., pages 234–296), paleoecology and diagenesis of Pleistocene limestone (G. E. Tebbutt, pages 297–331), and distribution of benthic Foraminifera (K. F. Wantland, pages 332–339) and Ostracoda (J. W. Teeter, pages 400–499). Another member of this group of doctoral scholars documented elsewhere the genesis of recent lime mud (Matthews, 1966). In addition, Purdy himself produced two thought provoking reports dealing with the origin of the topographic relief of the Belizean reef and its influence on sediment distribution (Purdy, 1974a, 1974b).

Among other studies of the Belizean reefs some of the most notable have been conducted by the University of Miami under the direction of R. N. Ginsburg. This work, to date, has focused on shallow-water submarine cements (Ginsburg and James, 1976; James et al., 1976) and has included geological investigations (James and Ginsburg, 1978) and a study of deep-reef fishes (Colin, 1974) of the deep seaward margins of the barrier reef and Glover's Reef atoll.

Several recent studies have concentrated on the barrier reef and the atolls. Devaney (1974) has reported on shallow-water echinoderms collected off Turneffe Island and Lighthouse and Glover's reefs. Wallace and Schafersman (1977) have examined the ecology and sedimentology of patch reefs in the Glover's Reef lagoon. This atoll was also the point of origin for a series of ichthyological studies that were expanded to the barrier reef complex and are still under way (Greenfield,

1972, 1975a–c, 1979; Greenfield and Greenfield, 1973; Greenfield and Johnson, 1981).

With the establishment of the Smithsonian Institution's field laboratory at Carrie Bow Cay in 1972, most of the marine research in Belize concentrated on this part of the barrier reef; only some early site surveys and comparative studies included other locations. Smithsonian-sponsored physiographic surveys (Dahl et al., 1974; Miller and Macintyre, 1977) were important early steps of our programs, while hurricane reports and damage and recovery surveys (Antonius, 1972; Stoddart, 1974; Highsmith et al., 1980) appear to have become a continuing necessity. Among the methods developed or modified during our reef research were mapping (Rützler, 1978a), underwater coring (Macintyre, 1975), and ecological sampling techniques (Dahl, 1973; KIRSTEuer, 1978; Rützler, 1978b; Rützler et al., 1980).

Early in our program, attempts were made to monitor the physical environment of Carrie Bow Cay and the surrounding waters. Cooperation with colleagues at the University of South Carolina who contributed specialized equipment produced information on the diurnal energy balance on the island (Kjerfve, 1978) and on tidal patterns relative to the Caribbean system (Kjerfve, 1981).

Inventory of flora and fauna was a prerequisite for the new program and produced an increasing number of checklists, distributional tabulations, taxonomic revisions, and descriptions of new taxa: algae and seagrasses (Tsuda and Dawes, 1974); nemerteans (Kirsteuer, 1974, 1977); polychaetes (Fauchald, 1980); sipunculans (Rice, 1976); copepods (H. B. Cressey, 1981; R. Cressey, 1981); ostracods (Kornicker, 1978, 1981; Kornicker and Cohen, 1978); decapods (Kensley, 1981; Kensley and Gore, 1981), bivalves (Waller, 1978), holothuroids (Pawson, 1976); echinoids (Kier, 1975); and fishes (Greenfield, 1981; Greenfield and Johnson, 1981; Johnson and Greenfield, 1982). A comparable inventory of novel chemical compounds from algae, sponges, and gorgonians is the subject of a series of publications of W. Fenical's group at Scripps Institution of Oceanography (McEnroe and Fenical, 1978; Mc-

Connell and Fenical, 1978; Kokke et al., 1979; Kokke et al., 1981).

Participants of several programs have examined organisms producing limestone and calcareous sand. Environmental influences on skeletal development of corals were studied by Barnard et al. (1974), Macintyre and Smith (1974), Graus and Macintyre (1976), and Highsmith (1979). Related work on mollusks has dealt with growth rates of gastropods (*Cerithium*: Houbrick, 1974) and shell calcification of bivalves (Arcoida: Waller, 1980). Calcium carbonate breakdown by biological processes, on the other hand, was the subject of studies by Rützler (1975), Rice (1976), and Highsmith (1981), and the contribution of noncalcareous (siliceous) components to reef sands was treated by Rützler and Macintyre (1978).

Another topic of research at Carrie Bow Cay has been the availability and quality of food as a major factor determining growth and distribution of invertebrates and fishes. Primary production by benthic algae, including spatial and temporal

variability, were discussed by Dahl (1974, 1976). Distribution of many algae is controlled by herbivores (Hay, 1981) but some plants can defend themselves from grazers by producing toxic compounds that act as feeding deterrents (Gerwick et al., 1979; Sun and Fenical, 1979; Paul and Fenical, 1980; Gerwick and Fenical, 1981). On the other hand, strong symbiotic ties exist between certain algae and invertebrates that were studied by Kokke et al. (1980) and Rützler (1981). Another report on invertebrate feeding presents behavioral observations on coronate medusae captured in plankton tows near Carrie Bow Cay (Larson, 1979).

The earlier work summarized here will give the reader an indication of research projects under way at the Carrie Bow Cay laboratory or sponsored by the Smithsonian reef study program elsewhere in Belize. The following papers in this volume will add further data and important new perspectives to our knowledge. Many more contributions can be expected to follow.

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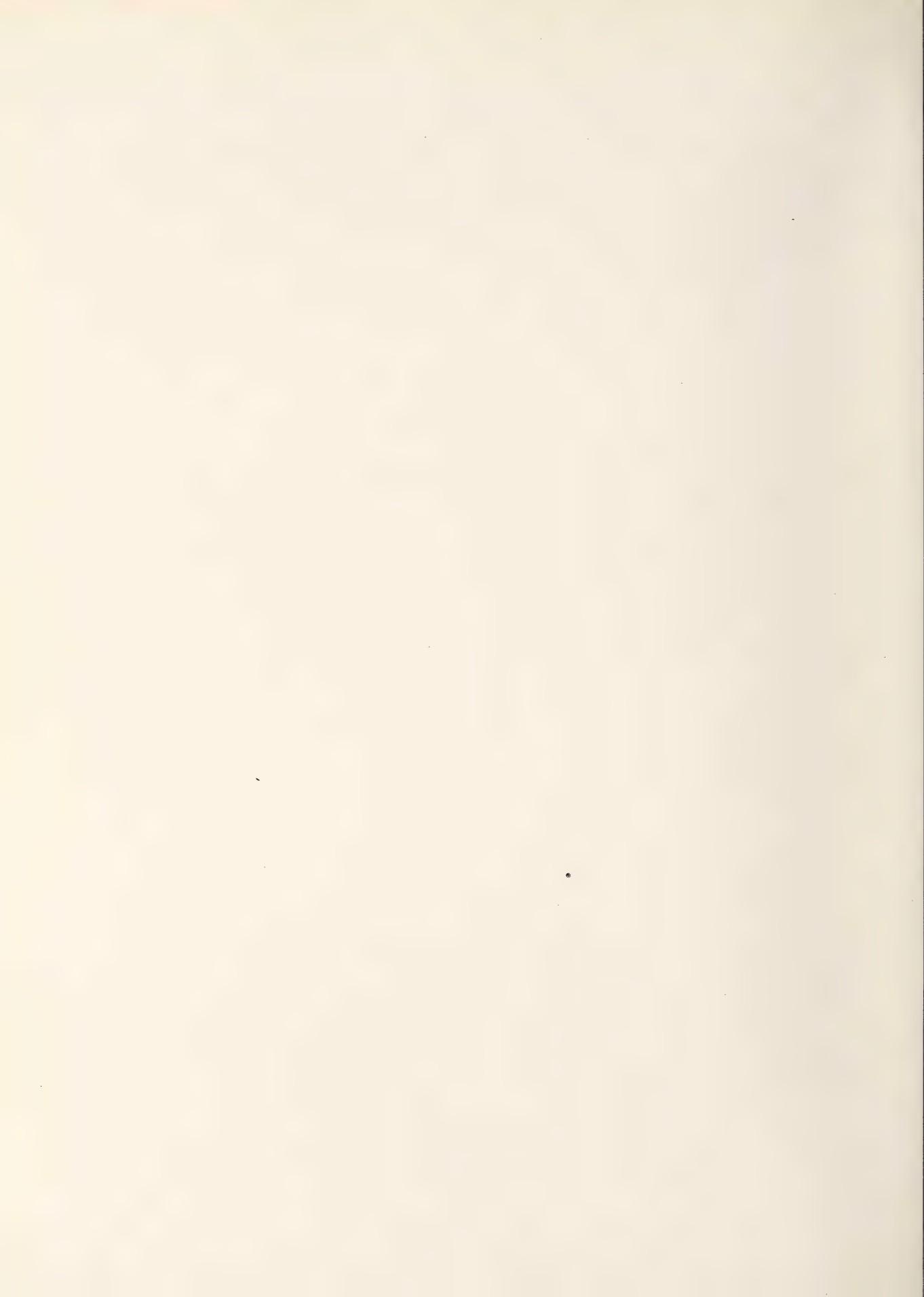
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# The Habitat Distribution and Community Structure of the Barrier Reef Complex at Carrie Bow Cay, Belize

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## ABSTRACT

The reef complex near Carrie Bow Cay, which is representative of the entire Belizean barrier reef, is separated from the mainland by a deep and wide lagoon, which grades into shallow seagrass bottoms, patch reefs, and mangrove cays on the outer barrier platform. A study transect west (lagoon) to east (open ocean) shows a distinct zonation of substrates and organisms that reflects primarily water depth and the prevailing wave and current regime. The shallow back reef shows massive coral growth, extensive pavement areas, and large rubble accumulations caused by hurricane surge; it is separated from the inner fore reef by a narrow intertidal reef crest pounded by waves. The inner fore reef (to 14 m depth) shows a characteristic spur and groove structure, with high buttresses in the shallow depth zone (to 10 m) and low-relief formations on the deeper terrace. The outer fore reef includes a steep inner-reef slope, a sand trough and an outer coral ridge. The steep fore-reef slope drops off at the top of the outer ridge. Many topographic features are comparable to those present on north Jamaican reefs. Corals of the genus *Acropora* suffer heavy damage but also gain wide distribution from storm swells. *Halimeda* plates dominate the coarse fraction of the sand substrates across the entire transect even far below the occurrence of the alga. Submarine pavement lithification is most pronounced in areas of low sediment accumulation. The outer ridge, although now dominated by

*Acropora cervicornis* on the study transect, appears to be built up by more solid framework. The reef at Carrie Bow Cay has a community composition representative of the central barrier reef province to which it belongs, but structurally it is a composite, including features characteristic of the discontinuous northern and southern province reefs.

## Introduction

The barrier reef complex—10–32 km wide (James et al., 1976) and approximately 250 km long—off Belize, Central America, is said to be the largest continuous reef in the Caribbean Sea (Smith, 1948; Adey, 1977). Beginning as a fringing reef off the Pleistocene peninsula of Ambergris Cay, it extends southward into the Gulf of Honduras. This reef complex consists of an almost unbroken barrier reef and numerous patch reefs and mangrove cays in its shoreward lagoon. The shelf lagoon is 20–25 km wide in the northern section of the complex, but where the lower third of the reef bends eastward towards Gladden Spit, the lagoon becomes more than 40 km wide before it opens into the Gulf of Honduras. The point at which the reef complex bends eastward is marked by two islets, one of which—Carrie Bow Cay—is the subject of this volume (Figure 1; Plate 1).

Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ), known as Ellen Cay up to 1944, is situated on top of the barrier reef proper, 22 km southeast of Dangriga (Stann Creek) (Figure 2) and 18 km east of Sittee

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FIGURE 1.—Tobacco Reef looking south toward South Water and Carrie Bow cays; note cuts isolating Carrie Bow Cay from barrier reef trend.

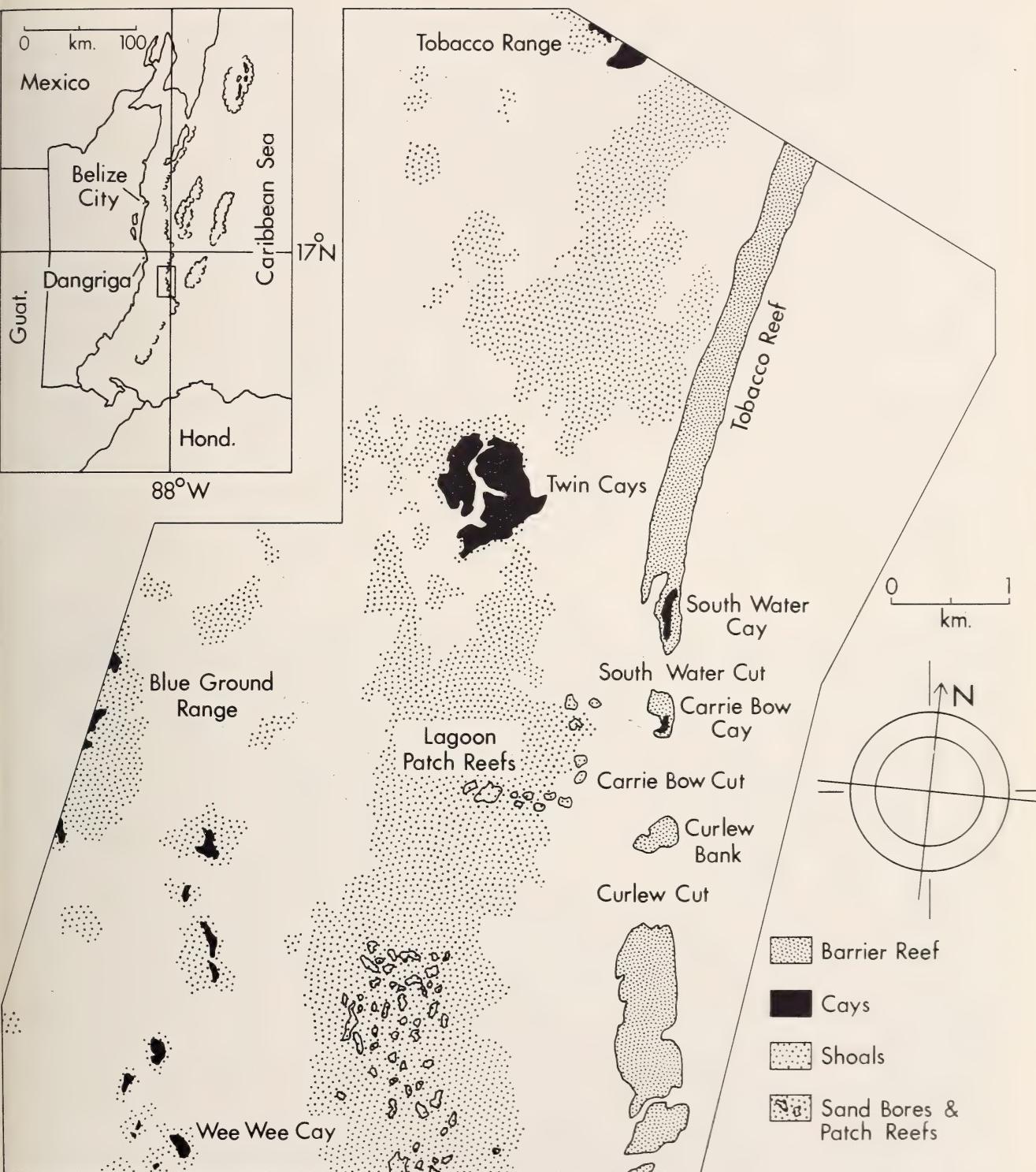


FIGURE 2.—Index map of barrier reef complex in the vicinity of Carrie Bow Cay; area of larger map located on inset by rectangle.

Point, which is the nearest land. Shoreward from Carrie Bow Cay, the eastern portion of the lagoon (on the barrier platform) is less than 5 m deep whereas the western part is as much as 20 m deep. The reef at Carrie Bow Cay (Figure 3; Plate 1: *center right*) is separated from the main barrier trend by two channels, South Water Cut to the north (0.4 km wide and 4 m deep) and Carrie Bow Cut to the south (0.7 km wide and 5 m deep). These and other channels through the barrier reef allow oceanic waters from the Caribbean Sea to flow onto the shallow barrier platform and to transport platform sediments to deep off-reef areas.

South Water Cut also separates Carrie Bow Cay (120 m long and 40 m wide) from the larger South Water Cay (440 m long and 100 m wide), a low island less than 1 km to the north that, like Carrie Bow Cay, is composed of reef rubble and sand. Twin Cays, locally known as Water Range,

is a swampy mangrove island 2 km to the northwest of Carrie Bow and is about 1 km in diameter and is divided by a meandering canal (Figures 3, 28a). Approximately 0.5–1.5 km west and southwest of Carrie Bow Cay and within the range of strong tidal currents passing through breaks in the barrier reef, numerous patch reefs having low relief occur among *Thalassia* seagrass in the shallow water (3–6 m) of the lagoon. Similar coral build-ups known as “sand bores” that reach the water surface and that are topped by intertidal sand are clustered about 3 km to the southwest.

Although many aspects of the Belize Shelf have already been studied and described—most notably by Stoddart (1963), Wantland and Pusey (1971), Purdy (1974), Purdy et al. (1975), and James and Ginsburg (1978)—most earlier work has been geologically oriented. In contrast, our description of reef zonation is based on detailed information about composition of flora and fauna



FIGURE 3.—Aerial view of Carrie Bow Cay looking northwest. South Water Cay (right) is a reef island on the barrier trend; Twin Cays (left) is a mangrove island in the shallow lagoon.

as well as topographic and substrate characteristics. Our study focuses on a 650 m research transect (just north of Carrie Bow Cay) that extends west to east from the lagoon to the deep fore reef and is representative of the entire barrier reef (Burke, herein: 509).

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## Methods

Vertical overlapping aerial photographs of the Carrie Bow Cay environs were made by a helicopter-mounted 70 mm camera with timed motorized film advance. Black and white or color prints ( $12 \times 12$  cm) were used to make photo composites (for instance, Frontispiece) from which topographic features could be traced on transparent overlays. The scales of the original maps, shown here in reduced figures, are 1:15,000 (Figure 2), 1:1500 (Figure 4), and 1:800 (Figure 5). Low-altitude aerial photographs (like Figure 8) were taken by balloon-suspended camera (Rützler, 1978a). The bottom topography in depths greater than eight meters is not discernible on aerial photographs and therefore had to be ascertained from underwater wide-angle photographs, as well as compass, depth-gauge, and tape measurements. Sediment thickness in each zone was determined with the aid of a steel probe (1 cm diameter) that could be extended in 3 m sections.

The study transect is approximately 200 m north of Carrie Bow Cay, midway across and perpendicular to the crescent-shaped reef crest that half encloses the island (Figure 4). Metal stakes driven into the coral and submerged and surface buoys anchored permanently mark the transect along its projected length (not bottom

contour) of 650 m. The zero point was established arbitrarily in a seagrass community in the shallow lagoon. Zones were determined on the basis of bottom configuration, substrates, and relative abundance of predominant organisms. Surveys were carried out along both the transect line and a 50 m strip on either side of it. Relative abundance of organisms within zones was measured by pointcounting organisms inside a  $0.25 \text{ m}^2$  frame randomly positioned (Rützler, 1978b:310, fig. 3). Objects overlayed by a 16-intersection grid (line stretched across every 10 cm) were recorded. Vertical projections of the points were used where the three-dimensional configuration of the substrate did not permit direct contact. In areas of high bottom relief, this method was more reliable and efficient than surface coverage estimates employed by Rützler (1975:206) for it avoids distortions due to nonhorizontal substrate surfaces (Dahl, 1973).

## The Transect

On the basis of dominant biological and geological characteristics, the barrier reef along the transect off Carrie Bow Cay can be divided into five major units: lagoon, back reef, reef crest, inner fore reef, and outer fore reef (Figure 5; Table 1). Each unit except for the reef crest can be subdivided into distinct zones. The movement and depth of water apparently are the main factors controlling the biological and geological zonations of this area. The lagoon unit (1.5–2.0 m depth) is marked by weak currents and a significant accumulation of fine sand and silt; the back reef (0.1–1.0 m) is subjected to strong currents and the lagoonward transportation of sediments; the water over the intertidal reef crest is in an almost constant state of agitation; the inner fore reef (1–12 m deep) similarly is strongly affected by both storm waves and waves related to normal trade wind conditions; the outer fore reef (at least 12 m deep), on the other hand, is affected only by long-period storm waves. Following is a detailed description of each unit.

**LAGOON.**—This environment consists of a sand and seagrass (*Thalassia*) zone (Figure 6) and a

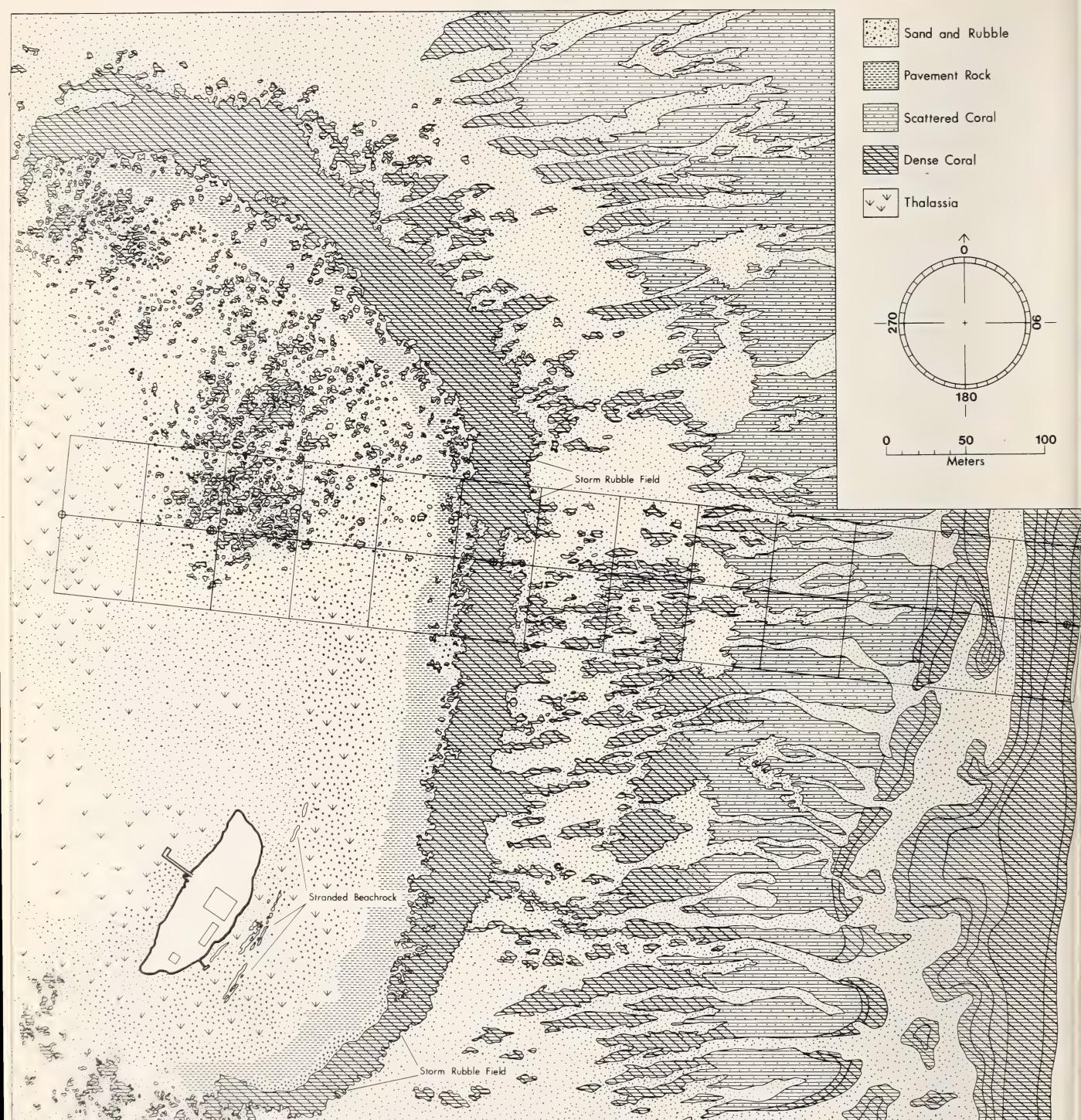


FIGURE 4.—Map of sea-floor characteristics of Carrie Bow reef with location of permanent study transect.

sand and rubble zone (Figure 7) that together extend only 50 m along the transect line. The first section, which extends for about 20 m from the zero point northwest of Carrie Bow Cay, covers a patch of seagrass (*Thalassia testudinum* Banks ex König, along with a few *Syringodium filiforme* Kützing) on a silty sand bottom (Figure 6a; Plate 2: top left). This sand is fair sorted, dominantly very fine to medium, and 1.0–1.2 m thick. It consists mainly of coral, mollusks, benthic Foraminifera (including *Homotrema*), and *Halimeda* plates. During one of our surveys (May 1975) the lower 10–15 cm of the plants were buried in sediments, presumably as a result of hurricane Fifi in 1974. The alga *Dictyota* sp., which was sparse in 1975, was very common during May and June of 1976, 1977, and 1978. Other algae regularly interspersed with *Thalassia* belong to the genera *Halimeda*, *Udotea*, and *Penicillus*. Empty conch shells and other rubble are covered by algal felts and patches of crustose coralline algae. Uncommon but conspicuous invertebrates include the anemone *Bartholomea annulata* (Lesueur) inside conch shells, the corals *Acropora cervicornis* (Lamarck) and *Siderastrea radians* (Pallas), the gastropods *Strombus gigas* Linnaeus and *Turbinella angulata* Lightfoot, the echinoid *Tripeutes ventricosus* (Lamarck), and the holothuroid *Holothuria mexicana* Ludwig. Benthic macroinvertebrates associated with this *Thalassia* community were studied by Young and Young (herein: 115).

Between 20 and 50 m along the transect, sand appears along with rubble (sand and rubble zone) largely covered by algal felts (13%) and by *Dictyota* spp. (6%) (Figure 7). The poorly sorted sediment in this zone ranges in size from silt to gravel and its composition is similar to that of sediments in the *Thalassia* zone. The metal probe recorded sediment thickness of 1.0–1.4 m over a hard bottom. *Acropora cervicornis* was absent from the sand and rubble zone in 1972, appeared in only two percent of samples by 1975 (but was very common in patches nearby, particularly just north of the transect), and by 1977 had taken over extensive areas on both sides of the transect (Figure

7a). A subsequent survey in spring 1979 after hurricane Greta (September 1978) showed that thickets of *A. cervicornis* had been broken up and carried deep into the lagoon by storm surge. New growth, however, was evident on some coral branches that had not been completely buried in sediment. During this survey, thick growths of the red alga *Champia parvula* (C. Agardh) Harvey (Norris and Bucher, herein: 201) appeared in patches throughout both the *Thalassia* and the sand and rubble zones (Figures 6b, 7b).

**BACK REEF.**—This unit, in which the bottom rises steadily from an average of 1 m to the intertidal reef crest, consists of a patch-reef zone (Figures 8, 9) and a rubble and pavement zone (Figure 11) that together extend from the 50 m mark to the 245 m mark along the transect. The substrate in the patch-reef zone (50–150 m marks) consists of gravel scattered in a poorly sorted silt to very coarse sand. The coarse fraction is composed mainly of *Halimeda*, coral, *Homotrema* and other benthic foraminiferans, mollusks, crustose coralline algae, and echinoids. Maximum sediment thickness recorded with the metal probe was 0.3 m. This zone is characterized by local build-ups of dead coral framework forming isolated patch reefs that consist primarily of *Montastrea annularis* (Ellis and Solander) and some *Diploria labyrinthiformis* (Linnaeus) and *Agaricia agaricites* (Linnaeus) (Figure 9). Approximately 50 percent of the surface area of the coral is dead and overgrown by crustose coralline algae and algal turfs (Figure 8). Characteristically, the vertical sides of many coral heads and boulders are alive but the top surfaces are dead, evidently because exposure at low tide has limited the upward growth of the corals. At the same time, considerable damage to this coral population is being caused directly or indirectly by the blue-green alga *Oscillatoria submembranacea* Ardisson and Strafforello (Antonius, 1973, 1977). Overhangs and crevices are commonly populated by the sea urchin *Diadema antillarum* Philippi, which, along with several species of parrot fishes, is responsible for extensive bioerosion of dead coral surfaces typical of this zone. Clusters of the corals *Acropora*

## Transect Across Barrier Reef at Carrie Bow Cay, Belize

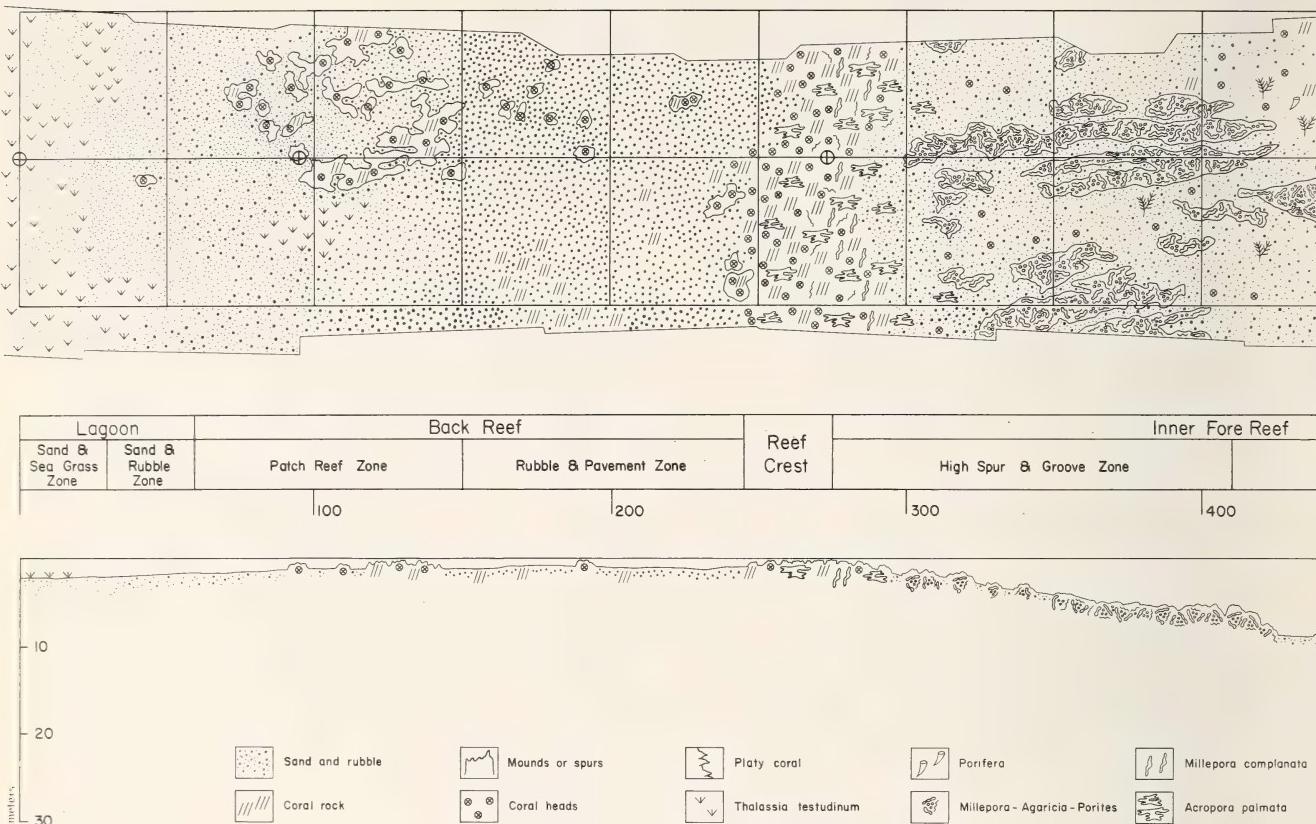
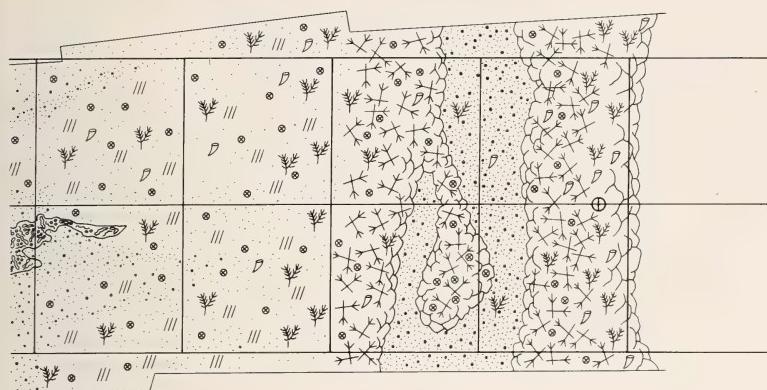


FIGURE 5.—Map and bottom profile of the permanent study transect with zonation terminology (+ = permanent markers).

*cervicornis* and *Porites astreoides* Lamarck, and the octocoral *Plexaura* spp. are dispersed throughout the sandy flats (Figure 8), with a variety of biota including *Dictyota* sp., *Cliona caribbaea* Carter, *Thalassia testudinum*, *Strombus gigas*, *Udotea flabellum* (Ellis and Solander) Lamouroux, *Amphiroa* sp., and *Penicillus capitatus* Lamarck—in order of abundance—growing in between. In the spring of 1979, as a result of hurricane Greta, most of the *A. cervicornis* showed extensive damage, and drifts of *A. cervicornis* debris were piled up against the patch reefs (Figure 10; Plate 2: center left). The corals *Acropora palmata* (Lamarck), *Porites porites* (Pallas), *Diploria strigosa* (Dana), *Siderastrea siderea* (Ellis and Solander), and *Agaricia fragilis* Dana were observed close to this zone but were not included in the counts.

The rubble and pavement zone appearing between 150 and 245 m along the transect consists of gravel in a silt to very coarse sand matrix that grades into a relatively smooth and undulating rock pavement adjacent to the reef crest (Figure 11). As can be seen on the map (Figure 4) the pavement is generally 40 m wide and forms the shoreward border of the entire reef crest trend. This pavement (described in detail by James et al., 1976) consists of a conglomerate of coral (*Millepora*), mollusk, and crustose coralline algal fragments lithified by a magnesium calcite submarine cement. We noted a maximum pavement thickness of only 4 cm although James et al. (1976) reported lithification down to 0.5–1.0 m in other areas of the barrier reef off Belize. Rock surfaces in this zone are overgrown by isolated



Low Spur & Groove Zone	Outer Fore Reef			
	Inner Reef Slope	Sand Trough	Outer Ridge	Fore Reef Slope
	500	600		meters



coral heads (*Siderastrea siderea* and *Porites astreoides*), scattered *Dictyota* spp., coralline crusts, and the boring sponge *Cliona caribbaea*. Less abundant organisms are algae of the genera *Halimeda*, *Caulerpa*, and *Penicillus* and the corals *Agaricia agaricites*, *Diploria clivosa* (Ellis and Solander), and *Acropora palmata*. The depth of water in this zone averages 0.6 m. *Acropora cervicornis* was abundant in this zone in spring 1978 (Figure 11a) but had nearly disappeared by the 1979 survey (Figure 11b), apparently owing to storm surges associated with hurricane Greta, which transported almost all living *A. cervicornis* lagoonward. Due south from the 150–200 m marks, between the transect and the island, the same zone changes into a *Thalassia*-dominated rubble flat, with *Porites porites*, *Siderastrea radians*, crustose corallines (on rubble), and *Diadema* (Plates 1: bottom right, 2: top right).

**REEF CREST.**—A transition zone (0.2 m deep) occurs between the back reef and fore reef at the 245–265 m marks along the transect. This zone is distinguished by a framework of dead (60%) and living *Acropora palmata* along with *Agaricia agaricites* and *Porites astreoides* (Figure 12; Plate 2: bottom left, bottom right). The bottom consists mainly of rubble and rock pavement covered by crustose coralline algae along with patches of fine to medium, well-sorted sand, the coarser fraction of which is mainly *Halimeda*, coral, *Homotrema*, and crustose coralline algae. This sand supports scattered growths of *Dictyota* sp. whereas the dead coral rock is commonly covered by algal turfs and dense stands of *Caulerpa racemosa* (Forsskål) J. Agardh. The section of the reef crest unit between 265 and 270 m along the transect (depth of 0.1 m) is dominated by the coral *Acropora palmata*, the hydrocoral *Millepora complanata* Lamarck, and the

TABLE 1.—Relative abundance of dominant organisms on the Carrie Bow Cay main transect (column heads designate region, structural and biological zone, transect position in meters from 0, depth in meters as average or range, and substrate in order of abundance; +++ =

	Lagoon		Back reef		Reef crest		
	Sand-mud	Sand-rubble	Patch reef-sand	Rubble-pavement	Coral rock-sand	Coral rock-rubble	Rubble-coralline rock
	<i>Thalassia</i>	Algal felts	<i>Montastrea-Diploria</i>	<i>Siderastrea-Porites</i>	<i>Acropora-Agaricia</i>	<i>Acropora-Millepora</i>	Corallines- <i>Millepora</i>
Biota	0-20	20-50	50-150	150-245	245-265	265-270	270-275
	2	1.8	1	0.6	0.2	0.1	0.1
	Muddy sand	Sand rubble	Sand rock rubble	Rubble rock sand	Rock sand rubble	Rock rubble	Rubble rock
Fleshy macro-algae	++	++	+	+++	++		
Calcareous macro-algae	++		+	++	++	+	
Crustose Corallinaceae			++	++	++	++	+++
Algal felts and turfs		+++	+	+	+	++	+
<i>Thalassia testudinum</i>	+++		+				
Massive Demospongea				++			
<i>Cliona</i> spp.				+			
<i>Millepora alcicornis</i>						+	+++
<i>M. complanata</i>						+++	+++
<i>Palythoa caribaeorum</i>							+++
<i>Stephanocoenia michelinii</i>							
<i>Madracis mirabilis</i>							
<i>Acropora cervicornis</i>	P	+	++	P			
<i>A. palmata</i>			P	+	+++	+++	
<i>Agaricia agaricites</i>			++	++	+++	+++	++
<i>A. fragilis</i>			P				
<i>A. lamarckii</i>							
<i>A. tenuifolia</i>							
<i>Leptoseris cucullata</i>							
<i>Siderastrea siderea</i>			P	+++	+		
<i>Porites astreoides</i>			++	+++	++	++	
<i>P. porites furcata</i>			P	+			++
<i>Diploria clivosa</i>				+	+		
<i>D. labyrinthiformis</i>			+++				
<i>D. strigosa</i>			P	P			
<i>Colpophyllia natans</i>							
<i>Montastrea annularis</i>			+++		P		
<i>M. cavernosa</i>							
<i>Meandrina meandrites</i>							
<i>Dichocoenia stokesii</i>							
<i>Dendrogyra cylindrus</i>							
<i>Mycetophyllia danaana</i>							
<i>Eusmilia fastigiata</i>							
<i>Erythropodium caribaeorum</i>							+
Erect Gorgonacea spp.			++	+			+
<i>Strombus gigas</i>			+				
<i>Diadema antillarum</i>			++	+			
Didemnidiae							

very common (>10% presence); ++ = common (5%–10% presence); + = less common (1%–5% presence); P = present and obvious but not encountered in the statistical samples)

Inner fore reef			Outer fore reef					
Spur and groove			Outer ridge					
Coral pin- nacles	High relief	Low relief	Inner reef slope	Sand trough	Inner slope	Top	Fore reef slope	
<i>Millepora</i> <i>Acropora</i>	<i>Agaricia-</i> <i>Acropora</i>	<i>Gorgonacea-</i> <i>Montastrea</i>	<i>Acropora-</i> <i>Monastraea</i>	<i>Gorgonacea-</i> <i>Montastrea</i>	<i>Acropora-</i> <i>Diploria</i>	<i>Acropora-</i> <i>Gorgonacea</i>	<i>Montastrea-</i> <i>Gorgonacea</i>	
275–330	330–410	410–550	550–575	575–615	615–625	625–645	645–655	
1.8	5	10	15–22	23	12–22	14	15–30	
Rock sand rubble	Sand rock rubble	Sand rubble rock	Rubble	Sand rubble	Rubble	Rubble sand	Rock rubble sand	
	++			+		+	++	
++		++			++		+	
	+			+			+	
+++		+++		+++	+	++	++	
	+	+					+++	
+++	++	+					+	
+		+					++	
	++	++					+	
+++	+++	+++			P	+++	+++	
	++	++			P		++	
+++	+++	++		+++			++	
					+		++	
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							++	
++	+	++		++			+	
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++	++	+		+			++	
P		+					++	
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	+				P		P	
		+			P		P	
					P		++	
			++				++	
			P				P	
	++	+++		+++	++	+++	+++	
							+++	



FIGURE 6.—Sand and seagrass zone before and after hurricane Greta: *a*, March 1978; *b*, April 1979. (Note extensive development of epiphytic red alga *Champia parvula* on *Thalassia testudinum* blades; scale = 40 cm.)

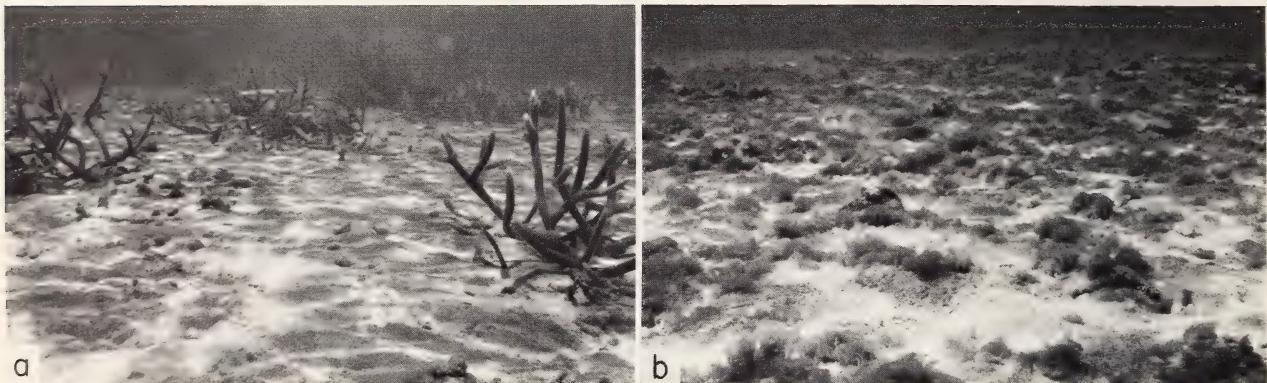


FIGURE 7.—Sand and rubble zone before and after hurricane Greta: *a*, March 1978, stands of *Acropora cervicornis* on plain substrate; *b*, April 1979, heavy red algal growth (*Champia parvula*) on substrate devoid of living *A. cervicornis*. (Scale = 40 cm.)

zoanthid *Palythoa caribaeorum* Duchassaing and Michelotti (Figure 13*a,b*; Plate 3: *top left, top right*). Coralline algal crusts, algal turfs, and *Porites astreoides* are attached to massive, extensively bored coral rock. The last windward section of the intertidal reef crest unit (270–275 m along the transect) is built up by rubble and coral rock (60%), covered by coralline crusts, *Palythoa caribaeorum*, *Millepora complanata*, some *Porites porites*, *Agaricia agaricites*, algal felts, and extensive crusts of the alcyonacean *Erythropodium caribaeorum* (Duchassaing and Michelotti). Just south of the tran-

sect line and at four or more other locations the reef crest is interrupted by perpendicular channels (Figure 13*c*), which facilitate the water exchange between lagoon and fore reef (Kjerfve, herein: 59).

At its southern limit, due southeast of Carrie Bow Cay, the reef crest zone grades into a coral-rubble storm ridge, which is actively accreting over the rubble and pavement zone (Figures 4, 14; Plates 2: *center right*, 5: *top left*). Our observations indicate that the shoreward transportation of this material occurs only during severe storms

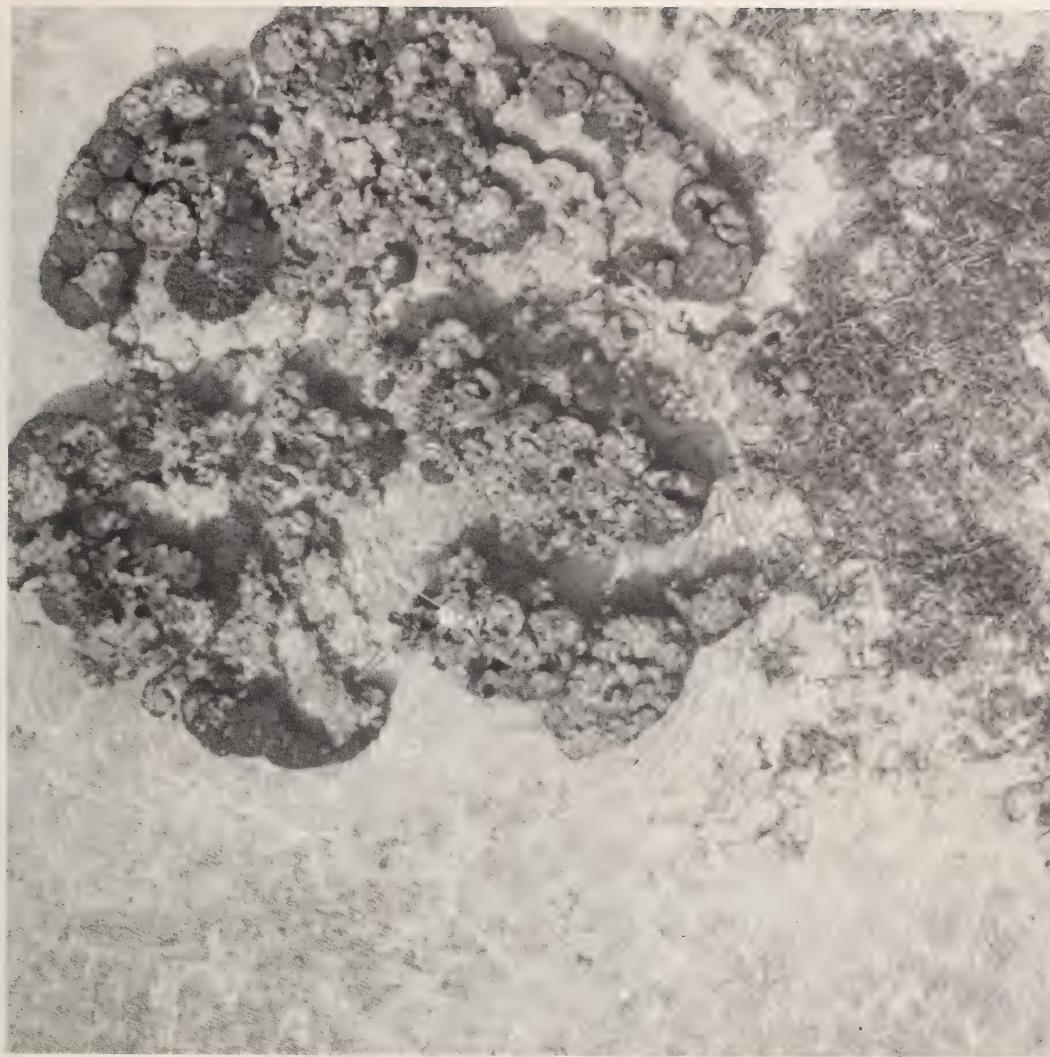


FIGURE 8.—Low-altitude aerial view of patch reef zone at the 100 m transect mark (lower center). Most of the patch reef is built up by *Montastrea annularis* (light areas are dead), accompanied by *Agaricia agaricites* and *Acropora cervicornis*; the latter also forms an extensive thicket on the right flank of the patch reef. (Picture area: 6 × 6 m.)

or hurricanes. During lesser storms this rubble is quite stable because much of it is platy (derived from *Acropora palmata*) and offers protection to a diverse interstitial invertebrate fauna (Plate 5: top right). Another comparable area on the reef crest is a small incipient rubble field located 50 m north of the transect line (Figure 4).

**INNER FORE REEF.**—Just east of the 275 m mark along the transect the bottom drops to a depth of 1.8 m and the inner fore reef begins in

a transition zone (to 330 m along the transect) of tall but unorganized coral pinnacles on a sand and rubble bottom (Figure 15; Plate 3: center left). These pinnacles are the result of turbulent water movement related to oscillating wave energy that is partly reflected by the reef crest. This area is comparable to Chevalier's (1973) Type II Outer Reef at Mururos, in which he related "pillar structure" of corals to heavy wave swell. Approximately half of these massive pinnacles off Carrie



FIGURE 9 (above).—*Montastrea annularis* patch reef on rubble substrate. Massive corals in this zone tend to form pedestal-shaped bases.

FIGURE 10 (below).—*Acropora cervicornis* thicket in patch reef zone badly damaged by hurricane Greta, September 1978. (Photograph taken April 1979.)



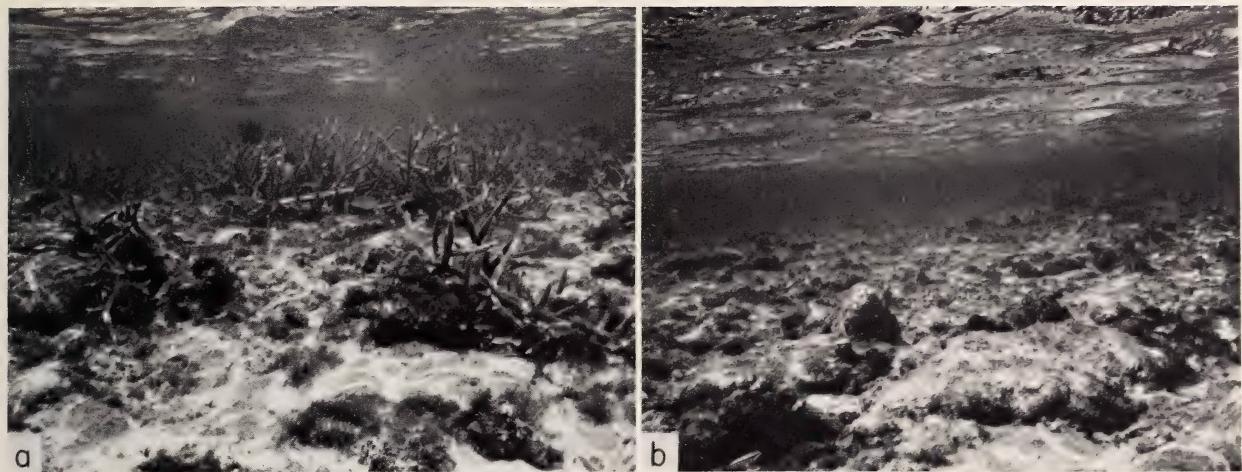


FIGURE 11.—Rubble and pavement zone before and after hurricane Greta: *a*, March 1978, extensive *Acropora cervicornis* and *Dictyota* sp. on sand and rubble bottom; *b*, April 1979, most of the dominant organisms and large quantities of sand have been transported lagoonwards. (Scale = 40 cm.)

FIGURE 12.—Inner margin of reef crest; algal turf covered coral rock surfaces show evidence of rasping action by parrot fish; *Caulerpa racemosa*, *Millepora complanata*, and *Porites astreoides* in foreground.



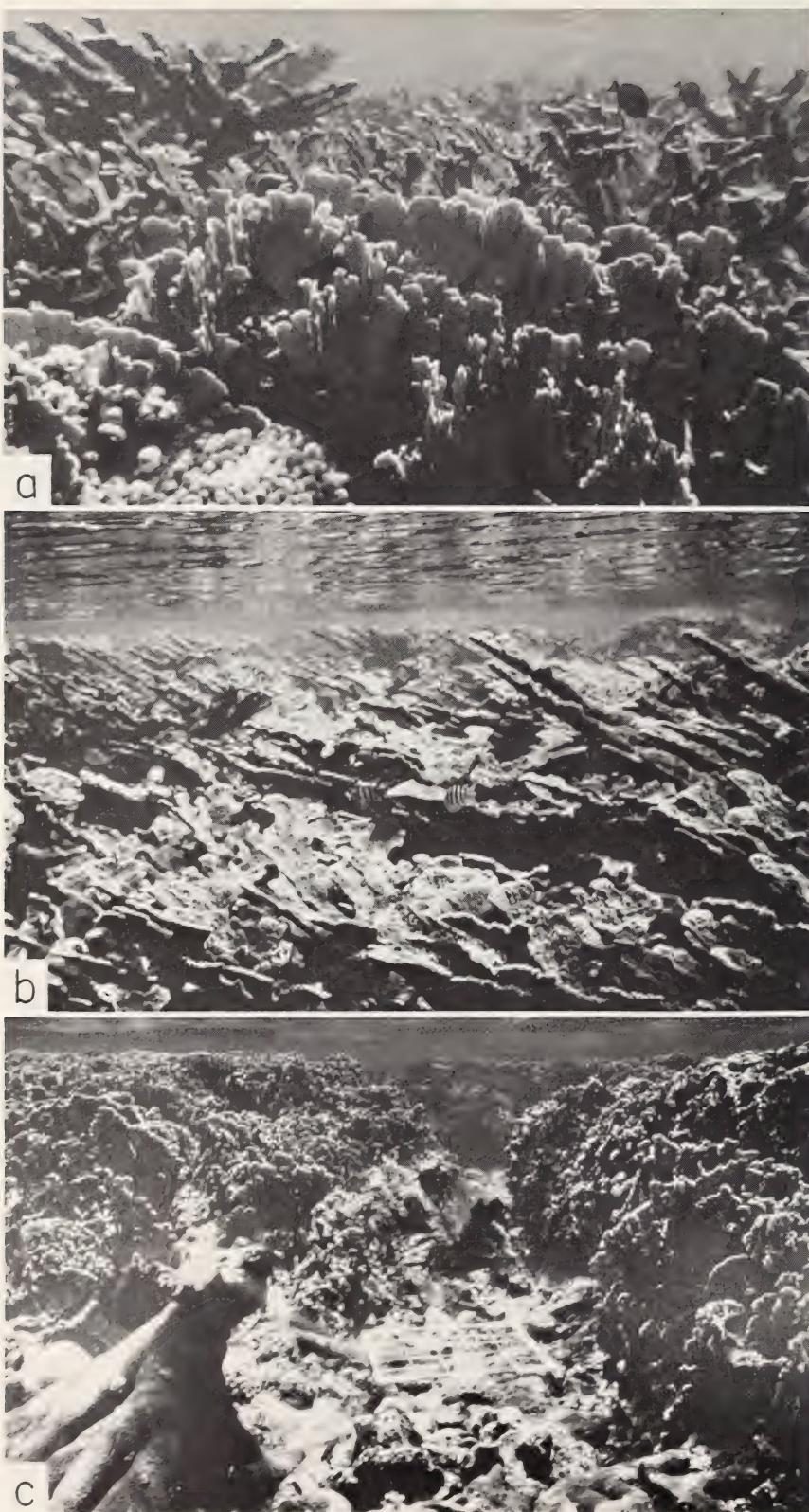




FIGURE 14.—Coral rubble storm ridge, south of the transect, photographed after hurricane Fifi (1974); rubble prograding over back-reef pavement, partly burying *Montastrea annularis* colony.

Bow Cay are formed by build-ups of dead *Acropora palmata*, the rest by live *Millepora complanata*, *A. palmata*, and *Agaricia tenuifolia* Dana. The dead framework is extensively covered by encrusting *Cliona caribbaea*, coralline algae, and some *Palythoa caribaeorum*. *Diploria strigosa*, *Porites astreoides*, *P. porites*, *Montastrea annularis*, and *M. cavernosa* (Linnaeus) are massive corals of secondary importance.

The spur and groove zone of high relief (330–410 m along the transect) has an average depth

FIGURE 13.—Seaward margin of reef crest: *a*, *Millepora complanata*, with *Porites porites* (foreground) and *Acropora palmata* (background); *b*, *A. palmata* community; *c*, Reef channel through *Millepora* ridge looking toward shallow inner reef crest (note overturned live colony of *A. palmata* in foreground). (Scale frame = 50 × 50 cm.)

of 5 m, but depth ranges from 3 to 10 m between the highest coral spurs and deepest sand grooves (Figure 16; Plate 3: center right). This well-defined zone has been discussed by Wantland and Pusey (1971) and has been described in detail by James et al. (1976). The high-energy oscillating movement of water in this zone has promoted coral growth on the spurs (Shinn et al., herein: 63) and has caused erosion in the grooves. The buttresses are characterized by foliate *Agaricia tenuifolia* and *Millepora complanata* enclosing clusters of *Porites porites* (Figure 17; Plate 3: bottom left). The tops of many buttresses are dominated by stands of *Acropora palmata* and *A. cervicornis* (Figure 18) and their flanks and the sand grooves in between by *Agaricia agaricites*, *Diploria strigosa*, various species of gorgonians (Muzik, herein: 303) and fleshy



FIGURE 15.—Pinnacles of *Millepora complanata* and *Agaricia tenuifolia* in an area of transition between reef crest and high-relief spur and groove zone.

green algae (Figure 16; Plate 3: center right, bottom right). Of lesser importance are *Siderastrea siderea*, *Porites astreoides*, *Dichocoenia stokesi* Milne Edwards and Haime and *Stephanocoenia michelinii* Milne Edwards and Haime. A characteristic and abundant—but quantitatively unimportant—component of this fauna is the purple hydrozoan *Stylaster roseus* (Pallas) that occurs in niches and overhangs along the sides of the buttresses. Another hydrozoan, *Millepora alcicornis* Linnaeus, commonly grows over the dead skeletons of gorgonians, mainly of *Gorgonia ventalina* Linnaeus. The medium sand to gravel-sized sediment in the grooves has a maximum thickness of 0.3 m. It has fair sorting and is composed mainly of coral, *Halimeda*, *Homotrema*, and mollusk and echinoid debris.

The spur and groove system of low relief extends between 410 and 550 m along the transect

(average depth, 10 m). A diverse population of gorgonians dominates the rock and rubble substrates of the sand flats as well as the low (about 1 m relief) coral spurs, which are formed of *Montastrea annularis*, *M. cavernosa*, *Acropora cervicornis*, and *Diploria strigosa* (Figure 19, 20; Plate 4: top left, top right). A few island-like coral pinnacles attain 3 m in height and diameter. Massive Demospongiae become quantitatively important in this zone of reduced agitation of near-bottom water, for example, *Neofibularia nolitangere* (Duchassaing and Michelotti), *Callyspongia* spp., *Aplysina* spp., *Geodia neptuni* (Sollas), *Ircinia* spp., as well as the thickly encrusting *Anthosigmella varians* (Duchassaing and Michelotti). *Halimeda* spp. and *Dictyota* spp. are common algae. Conspicuous corals having patchy distribution are *Agaricia agaricites*, *A. tenuifolia*, *Diploria labyrinthiformis*, *Dendro-*



FIGURE 16.—High-relief spur and groove zone, having 5 m relief. (Water depth at sand bottom: 6 m.)

*gyra cylindrus* Ehrenberg, and *Eusmilia fastigiata* (Pallas). Probes of the sand-filled grooves indicated a maximum depth of 1.2 m at the shallow end of this zone. Seaward, these sand lenses thin out and eventually give way to sand pockets in a rock pavement. The sediment is similar to that found in the high-relief spur and groove zone. James et al. (1976:532) referred to this low-relief spur and groove zone as the "deep spur and groove," which was described as being separated from a "shallow spur and groove" system by a "rubble-covered terrace." There is no indication, however, that a terrace separates the high- and low-relief spur and groove zones off Carrie Bow Cay. In fact, the spurs having low relief are commonly a continuation of the shallower high-relief spurs, with one or more shallow grooves spilling into one of the deeper and wider grooves.

Furthermore, the relief of the spurs is considerably less than that reported by James' group who described spurs having relief of 3–4 m that rise to within 2 m of the surface of the waters.

**OUTER FORE REEF.**—This region begins with a 25-degree slope—the inner reef slope—where the transect drops from 15 m depth at 550 m along the transect to 22 m at a position 575 m along the transect. Most of the bottom is covered by a thicket of living and dead *Acropora cervicornis* that offers substrate to some massive sponges—*Verongula gigantea* (Hyatt), *Callyspongia vaginalis* (Lamarck)—and various gorgonians. Columnar colonies of *Montastrea annularis* at the top of the slope give way to large platy colonies towards the base that are accompanied by *Porites astreoides*, *Siderastrea siderea*, and *Agaricia tenuifolia* (Figure 21; Plate 4: center left). Very poorly sorted sediment com-

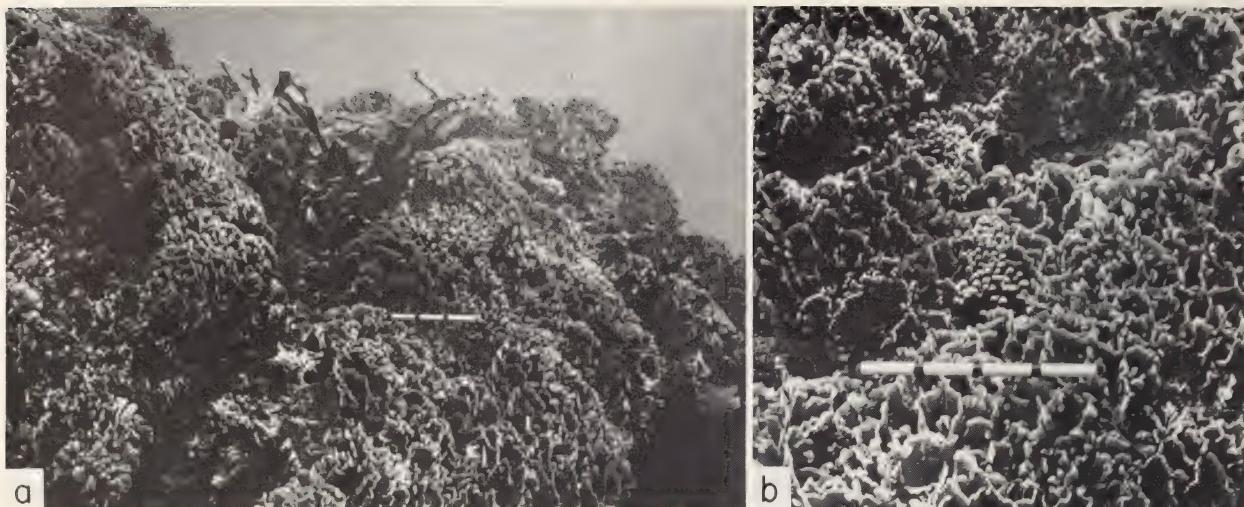


FIGURE 17.—Dominant framework builders of buttresses in high-relief spur and groove zone: *a*, *Agaricia tenuifolia* capped by *Acropora palmata*; *b*, close-up view of characteristic coral association consisting of *A. agaricites*, *Millepora complanata*, and *Porites porites*. (Scale = 40 cm.)



FIGURE 18.—*Acropora palmata* development on top of buttress in high-relief spur and groove zone. (Depth: 4 m.)



FIGURE 19.—Low-relief spur and groove zone with scattered coral heads (foreground: *Montastrea annularis*) among octo corals on the rock pavement of a low spur. (Depth: 10 m.)

FIGURE 20.—Sand-covered hard ground dominated by octocorals with islands of coral heads, near outer edge of low-relief spur and groove zone. (Depth: 13 m.)

posed of silt to medium-sized sand with scattered coarser debris, occurs in patches on this slope. *Halimeda* plates, mollusks, and echinoid spines make up most of the readily recognized coarse fraction. This inner reef slope is comparable to "the steep coral-veneered rock slope" that James and Ginsburg (1978:33-35) called the "reef step."

The next section along the transect is a sand trough 40 m wide (575-615 m marks) and an average of 23 m deep (Figure 22). The substrate is a poorly sorted, silt size to very coarse sand sediment plain. This sediment is mainly very fine to fine sand, but coarser material consisting of





FIGURE 21.—Platy coral development (*Montastrea annularis*) at base of inner reef slope; note brick with coral transplant (Graus and Macintyre, herein: 441). (Depth: 21 m; scale = 40 cm.)

*Halimeda* plates, mollusks, benthic foraminiferans, and echinoids is scattered throughout. Probings indicated that sediment varies in thickness from about 1 m at the toe of the inner reef slope to more than 12 m in the axis of the trough. Pieces of rubble support gorgonians and sponges, as well as some corals that form several small, isolated coral patches, predominantly of *Montastrea annularis* and *M. cavernosa* (Figure 22a). This sand trough zone on the transect also encompasses one tall coral pinnacle in the western part of the trough that has a coral-gorgonian composition similar to that of the inner slope with which it is connected by a low *Acropora cervicornis* ridge (Figure 4). This zone correlates with the seaward-dipping sediment terrace off Tobacco and Buttonwood cays, where the slope is not bordered by an outer ridge (James and Ginsburg, 1978).

At Carrie Bow Cay an outer ridge runs parallel to the intertidal reef crest and delineates the continental shelf (Figure 4). On the transect it is formed mainly by a thicket of *Acropora cervicornis* (Figures 22b, 23a), but south of the Carrie Bow transect *Montastrea annularis* becomes the principal framework builder (Figure 23b). The steep 45-degree landward slope of the outer ridge (Figure 22b) supports, among the branches of *A. cervicornis*, massive *Diploria labyrinthiformis*, *Porites astreoides*, and *Stephanocoenia michelinii*, gorgonians, large sponges—*Pseudoceratina crassa* (Hyatt), *Xestospongia* sp.—and conspicuous algae—*Halimeda* spp., *Stylopodium zonale* (Lamouroux), *Peyssonnelia* sp. The top of the outer ridge lies between 625 and 645 m along the transect and its depth ranges from 12–14 m (Figure 23a). *Acropora cervicornis* and gorgonians are the dominant organisms, with



FIGURE 22.—Sand trough: *a*, isolated coral patches at the base of inner reef slope, 23 m deep; *b*, view from the top of the outer ridge over *Acropora cervicornis* thicket, 12 m relief.





FIGURE 24.—Fore-reef slope: *a*, looking up sand shoot from 25 m; *b*, platy coral-octocoral community on transect at 30 m.

local accumulations of *Montastrea annularis*, *Agaricia agaricites*, *A. tenuifolia*, and *Madracis mirabilis* (Duchassaing and Michelotti). Fleshy green algae, and sponges of the genera *Aplysina*, *Verongula*, *Callyspongia*, *Xestospongia*, and *Agelas* are common associates (Plate 4: center right). Poorly sorted, very fine sand to gravel-sized sediments that are rich in *Halimeda* plates occur in small, 1 m deep depressions scattered along the crest of the ridge. An identical shelf-edge ridge occurs off South Water Cay (James and Ginsburg, 1978).

Approximately 645 m along the transect, the fore-reef slope (Figure 24) drops at an angle of 50°–70° from depths of 14 m down to 30–60 m,

FIGURE 23.—Outer ridge: *a*, coral community dominated by *Acropora cervicornis* on transect line, 12 m depth; *b*, platy *Montastrea annularis* and *Porites astreoides* framework 100 m south of transect, 14 m depth. (Scale = 40 cm.)

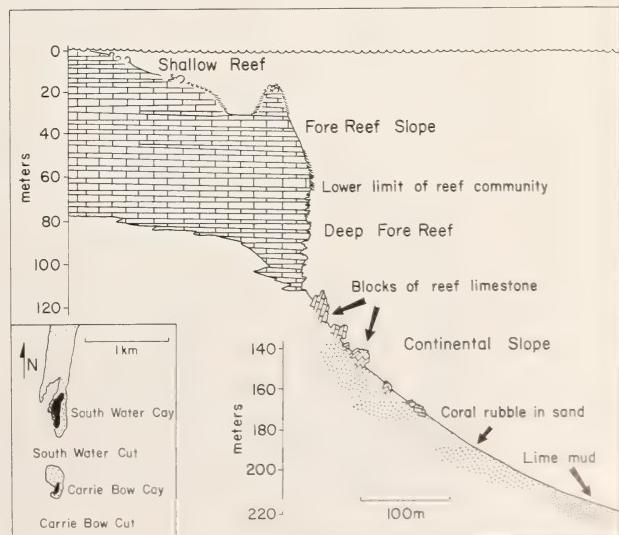


FIGURE 25.—Profile and dominant sea-floor characteristics of fore reef off South Water Cay (adapted from James and Ginsburg, 1978).

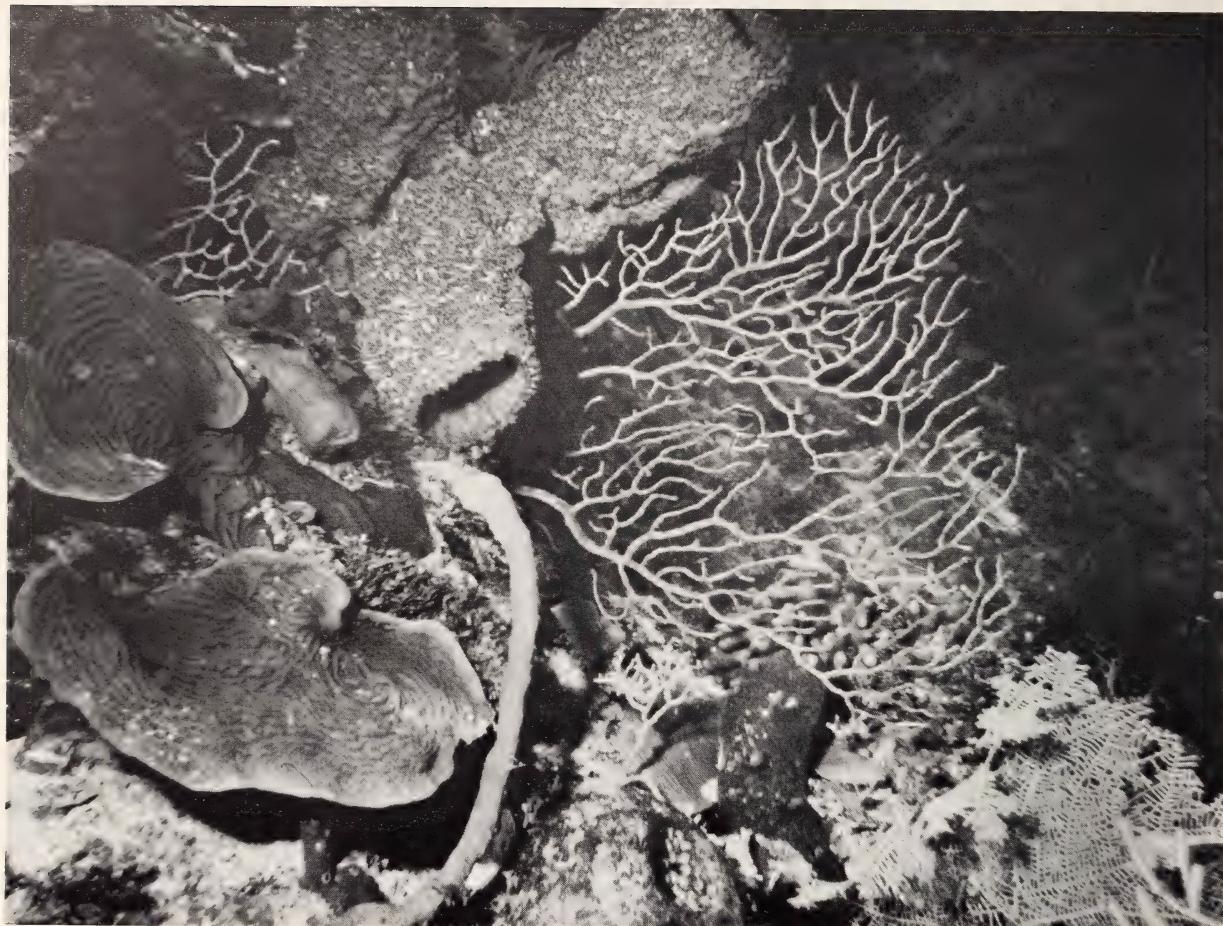


FIGURE 26.—Close-up view of representative fore-reef slope community of sponges, corals, and octocorals, including (clockwise from center bottom) *Cinachyra kuekenthali*, *Amphimedon compressa*, *Agaricia lamarcki*, *Mycale* sp., *Iciligorgia schrammi*, *Porites porites*, *Pseudopterogorgia* sp., and encrusting *Millepora* sp. (Depth: 30 m.)

where it diminishes to 40°–50°. According to previous observations from the research submersible *Nekton* off nearby South Water Cay (James and Ginsburg, 1978), a vertical wall continues from a depth of 60 m to about 110 m where a talus of large reef limestone blocks, coral rubble, and *Halimeda* sand grades into a gently sloping lime-mud bottom at about 200 m (Figure 25). Our surveys, which were restricted to a maximum depth of 30 m, show an abundance of platy *Montastrea cavernosa* and *M. annularis*, Gorgonacea, *Agaricia fragilis*, *Leptoseris cucullata* (Ellis and Solander), and Demospongea (Figures 24b, 26, 27; Plate 4: bottom left, bottom right). Commonly asso-

ciated are *A. agaricites*, *A. lamarcki* Milne Edwards and Haime, *Porites porites* forma *furcata* Lamarck, *Diploria labyrinthiformis*, *Colpophyllia natans* (Houttuyn), and *Mycetophyllia danaana* Milne Edwards and Haime. Abundance of gorgonians decreases with depth whereas that of sponges increases. A conspicuous gorgonian under 20 m is *Iciligorgia schrammi* Duchassaing (Figure 27). Quantitatively important sponges are rope-shaped species of *Aplysina*, *Niphates*, and *Haliclona*, tubular *Agelas* sp. and *Verongula* sp., massive *Ectyoplasia ferox* (Duchassaing and Michelotti) and *Cinachyra kuekenthali* Uliczka, and coral-eroding *Cliona delitrix* Pang and *Siphonodictyon coralliphagum* Rützler. Hal-



FIGURE 27.—Vertical fore-reef slope with platy development of *Montastrea cavernosa* and abundant sponges and octocorals. (Depth: 40 m.)

TABLE 2.—Abundance of various benthic components (major substrates and predominant functional groups) compared by habitats of the barrier reef transect and the lagoon (number of counting points beneath zone names; +++ = very common; ++ = common; + = less common; +− = rare; − = not in samples; average abundance values (%) from point counts, if available, in parentheses; \* = >100% total because corallines and their rock and rubble substrate were recorded separately)

Benthic components	Barrier reef transect				Off-transect lagoon			
	Lagoon 176	Back reef 368	Reef crest* 272	Inner fore-reef* 640	Outer fore-reef 480	Seagrass flats 0	Mangrove 0	Patch reefs 320
SUBSTRATE								
Mud	−	−	−	−	−	+	+++	−
Sand	+++ (55.7)	+++ (15.4)	+	(2.2)	+++ (12.0)	++ (9.6)	+++	+++ (28.2)
Rubble, boulders	++ (6.8)	+++ (17.4)	+++ (10.3)	+++ (18.8)	+ (4.2)	+− (1.9)	−	+
Rock	−	+++ (14.7)	+++ (47.8)	+++ (16.3)	+++ (14.2)	−	−	+++ (14.7)
Mangrove roots	−	−	−	−	−	−	+++	−
FUNCTIONAL GROUP								
Marine grasses	+++ (22.2)	+− (0.5)	−	−	−	+++	+++	++ (8.5)
Fleshy macro-algae	+++ (13.6)	++ (8.2)	+	(3.7)	+− (0.9)	+	+++	++
Calcareous macro-algae	+− (0.6)	++ (6.8)	+	(2.6)	+	(3.8)	++	−
Crustose Corallinacea	−	++ (5.2)	+++ (35.6)	++ (5.6)	+ (1.9)	+	++	−
Massive Demospongea	−	−	−	+	+ (2.7)	+	++	−
Excavating sponges	−	+ (3.0)	−	+	+ (5.0)	+	++	++ (8.5)
Hematypic corals	+− (0.6)	+++ (24.5)	+++ (31.6)	+++ (35.9)	+++ (30.0)	−	−	−
Gorgonacea	−	++ (3.8)	+(1.1)	++ (6.1)	+++ (18.5)	−	−	+++ (17.2)
Others	+− (0.6)	+− (0.5)	+− (0.7)	+− (0.5)	+− (0.8)	+− (0.7)	+	+− (0.7)

*imeda*-rich, very fine sand to gravel-sized sediment occurs in pockets or small ledges between the living cover of this slope. Other components of this sediment include mollusks, echinoids, corals and benthic foraminiferans.

### Lagoon Environment

Reef-forming organisms and other characteristic and quantitatively prominent associates observed on the barrier reef transect off Carrie Bow Cay are all sessile and require stable substrates to keep them from being washed away. In the protected lagoon fine sediments tend to bury such substrates and, by settling on organisms as well, constitute a selective stress factor for the living populations. Thus, we examined the lagoon within a radius of 2 km from Carrie Bow Cay in order to compare its characteristic benthic biota with those of the barrier reef (Table 2). A similar comparison of zooplankton is presented by Ferraris (herein: 143) and complemented by Rützler et al. (1980). Although seagrass flats and mangroves were surveyed only qualitatively, patch reefs were examined both quantitatively and qualitatively. The Carrie Bow Cay reef flat (between the cay and the reef crest) is the subject of a separate detailed study (Rützler, in prep.).

**SEAGRASS COMMUNITY.**—An area of approximately 6 km<sup>2</sup> of lagoon bottom immediately due west of Carrie Bow Cay was found to be less than 6.5 m deep, commonly 4–6 m deep. More than 90 percent of this area is flat soft bottom covered by *Thalassia testudinum*; the rest consists of rubble, reef patches, and large sponges. Most of the rubble originates from the commercial conch *Strombus gigas*. The shells, abandoned by fishermen in large piles or fields, provide substrate for a variety of algae (for instance, *Amphiora fragilissima* (Linnaeus) Lamouroux), sponges (*Desmapsamma anchorata* (Carter)), hydrocorals (*Millepora* sp.), corals (*Porites* sp., *Siderastrea siderea*), gorgonians (*Plexaura* sp.), and many less conspicuous organisms. The dark interior of these shells constitutes a well-ventilated miniature cave habitat because fishermen puncture the spire near the apex where they cut the retractor muscle to remove the soft

parts of the snail. Extent of colonization depends on exposure time and position of aperture relative to the sediment substrate. Small reef fishes, encrusting coralline algae, foraminiferans (*Homotrema rubrum* (Lamarck)), sponges (*Spirastrella* sp., *Clathrina* sp.), bryozoans and ascidians, as well as anemones (*Bartholomea annulata*), crabs (*Mithrax* sp.), and ophiuroids (*Ophiotrix* spp.) are common inhabitants. Several species of *Cliona* excavate the walls of old shells, some of which are occupied by the hermit crab *Petrochirus diogenes* (Linnaeus).

Distribution of living conchs is patchy and their depletion in large areas observed by us over a seven-year period indicates over fishing. On the other hand we noted concentrations near certain conch rubble patches comparable to those reported by Hesse (1979). Another large gastropod, *Turbinella angulata*, is a common associate. Sponges are quantitatively the most important organisms in the *Thalassia* meadows, even outside the rubble fields. In 1975 and 1978 many were found loose and only partly alive, together with gorgonians in similar condition (Muzik, herein: 303) and can be assumed to have been torn from the reef and washed into the lagoon by hurricane surge (Rützler and Ferraris, herein: 77). The presence of recently sunken coconut trees confirms this assumption. Other sponges, however, were healthy and attached to small pieces of rubble and seagrass (*Desmapsamma anchorata*, *Iotrochota birotula* (Higgin), *Aplysina fistularis* (Pallas), *Niphates erecta* Duchassaing and Michelotti) or, like some very large forms (5–40 l volume), were rooted in sand (*Spheciopspongia vesparium* (Lamarck), *Ircinia* spp.).

**PATCH REEFS.**—These lagoon reefs of low relief are clustered about 0.3–2.0 km to the west and southwest of Carrie Bow Cay (Figure 2). Favorable substrate conditions, together with trade-wind and tide-induced currents passing through South Water and Carrie Bow cuts probably promoted the development of these structures that now exhibit a richness of reef fauna that is surpassed only by the outer barrier fore reef. Diversity and biomass of sponges, in particular, are higher than in any other habitat of similar depth because most species favor areas having a high rate of water exchange but lack resistance against



FIGURE 28.—Twin Cays: *a*, aerial view of mangrove island showing channel and intertidal mud flats behind red mangrove fringes; *b*, red mangrove (*Rhizophora mangle*) on mud bank bordering channel.

detachment from substrates by undulating water movement. The patch reefs are circular or oval, some are arranged in string-of-pearl fashion, 5–60 m in diameter and raised 0.2–1.0 m above the surrounding flat sand and *Thalassia* bottom in

depths of 3–6 m. Abundance data were derived from two perpendicular transects across a characteristic patch reef, named “Spaghetti Reef,” after a new species of stringy sponge of the genus *Ulosa* (Rützler, 1981). Sand and coral rock make



FIGURE 29.—Seagrass community of the shallow lagoon at the entrance to Twin Cay channel: *Thalassia testudinum*, *Halimeda incrassata*, and *Manicina areolata*. (Depth: 1 m.)

up 45% of the surface area. Gorgonians are the most abundant organisms (20%), followed by corals and milleporids (17%), sponges (9%), and *Thalassia* seagrass (on sand, 9%). Large algae are notably absent. *Gorgia ventalina* and *Pseudopterogorgia* spp. are the most conspicuous octocorals on the patch reefs. Massive forms dominate among the corals (*Siderastrea siderea*, *Diploria labyrinthiformis*, *D. strigosa*, *Montastrea annularis*), the most common hydrocoral is *Millepora alcicornis*, which encrusts numerous gorgonian skeletons. Sponges, although they score comparatively low in the point counts, contribute most to the standing crop. The principal species are *Ircinia* spp., *Xestospongia* sp., *Iotrochota birotula*, *Desmapsamma anchorata*, *Amphimedon compressa* Duchassaing and Michelotti, and *Callyspongia* spp. (Plate 5: center left, center right).

**MANGROVE.**—Toward Twin Cays from the southeast a belt of shallow (1 m) *Thalassia* flat grades into the larger entrance of the channel that divides this island (Figure 28a). The flat is a transition zone between the more agitated deeper lagoon and the protected mangrove where moderate tidal currents control water exchange. Most abundant among the *Thalassia* are some algae (for instance, *Penicillllus capitatus*, *Halimeda incrassata* (Ellis) Lamouroux), sponges (*Tedania ignis* (Duchassaing and Michelotti), *Oligoceras violacea* (Duchassaing and Michelotti), *Haliclona viridis* (Duchassaing and Michelotti)), and the coral *Manicina areolata* (Linnaeus) (Figure 29). *Millepora* sp. encrusts large surface areas of submerged wood. Some more sponges, *Aplysina fulva* (Pallas) and the large loggerhead *Spheciospongia vesparium*, and numerous starfish (*Oreaster reticulatus* (Lin-

naeus)) occur on the bottom of the channel entrance.

The meandering channel is 0.5–2.0 m deep and is lined by red mangroves, *Rhizophora mangle* Linnaeus, which grow on intertidal mud banks and extend their arched prop roots into subtidal water (Figure 28b). In places the mud banks are washed out to form vertical walls and even overhangs and caves. Mud caves, probably of similar origin, are found outside the present mangrove margin just north of Twin Cays. They extend horizontally into mud banks surrounding 4 m depressions in the seagrass floor. The caves are large enough to harbor 2 m long sharks.

Mangrove roots offer the only substrates that are not subject to accumulation of fine sediments. In this habitat strong competition for the limited space takes place among diverse flora and fauna (Figure 30). On the light-exposed roots and bank edges, clusters of the algae *Caulerpa verticillata* J. Agardh and *Halimeda* spp. compete with the sponges *Tedania ignis*, *Ircinia felix* (Duchassaing and Michelotti), and *Lissodendoryx* sp. (Figure 30a,b; Plate 5: bottom left, bottom right). The walls of the shaded overhangs are dominated by the sponge *Ulosa ruetzleri* Wiedenmayer and, at the north entrance of the channel, by *Mycale* sp. Also, locally important in biomass are the anemones *Bartholomea annulata* and *Condylactis gigantea* (Weinland), the tunicates *Ecteinascidia turbinata* Herdman and *Ascidia nigra* (Savigny), and sabellid polychaetes. The intertidal parts of the mangrove roots are dominated by the oyster *Crassostrea* sp., whereas the *Thalassia* mud bottom supports a dense population of Scyphomedusae (*Cassiopea* spp.), with specimens of *Oreaster reticulatus* interspersed (Figure 30c). Mud caves and roots provide hiding places for a diverse fish fauna (Figure 30b).

### Summary and Conclusions

This paper presents the first detailed description of the biological-geological zonation of the barrier reef complex off Belize. Despite some variation along the barrier reef (see Burke, herein), the zonation of the Carrie Bow Cay

segment is typical of the entire reef platform (Figures 4, 31). Except for its large lagoon and greater distance from land, the Belizean barrier reef is comparable to well-investigated fringing barrier reefs off the north coast of Jamaica (Goreau, 1959; Goreau and Land, 1974).

Seaward of the *Thalassia*-dominated lagoon, the back reef occurs between an area of massive coral heads on rock pavement and the breakers of the reef crest (Figure 31). On our transect we did not consider this "reef flat" as part of the crest (Goreau, 1959:74) because, although this zone is intertidal, it is very narrow and almost always flooded by waves; instead, we defined "reef flats" herein as large intertidal areas between the eastern shores of South Water and Carrie Bow cays and their nearby crests (Larson and Larson, herein; Rützler, in prep.). Only the narrow intertidal breaker zone is included in the reef crest. The inner fore reef begins at this point with a spur and groove (= buttress) zone of high relief—which in Jamaica is considered a part of the crest (Goreau, 1959)—but it changes abruptly into a gently sloping terrace of spurs and grooves having low relief ("seaward slope" or "upper fore-reef terrace" in Jamaica). The outer fore reef on our transect has a steep inner reef slope, a perpendicular sand trough parallel to the reef crest, and an outer coral ridge where the fore-reef slope begins to drop off to the deep (vertical) fore reef. The comparable feature off Jamaica is a lower fore reef having a lower fore-reef escarpment. Both the trough and the ridge are missing in Jamaica (Goreau and Land, 1974).

Water movement (direction and force) appear to control the development of zonation patterns. Wave action determines not only reef types, by influencing coral zonation (Geister, 1977), but also influences the distribution of all other sedentary organisms, some of which—for instance, octocorals, sponges, and algae—have considerable ecological importance. The quantitative significance of many coral associates is undervalued by most field methods (point and chain-link counts, estimates of area coverage) because presence or surface area is measured but not biomass (massive sponges) or space occupied (swaying

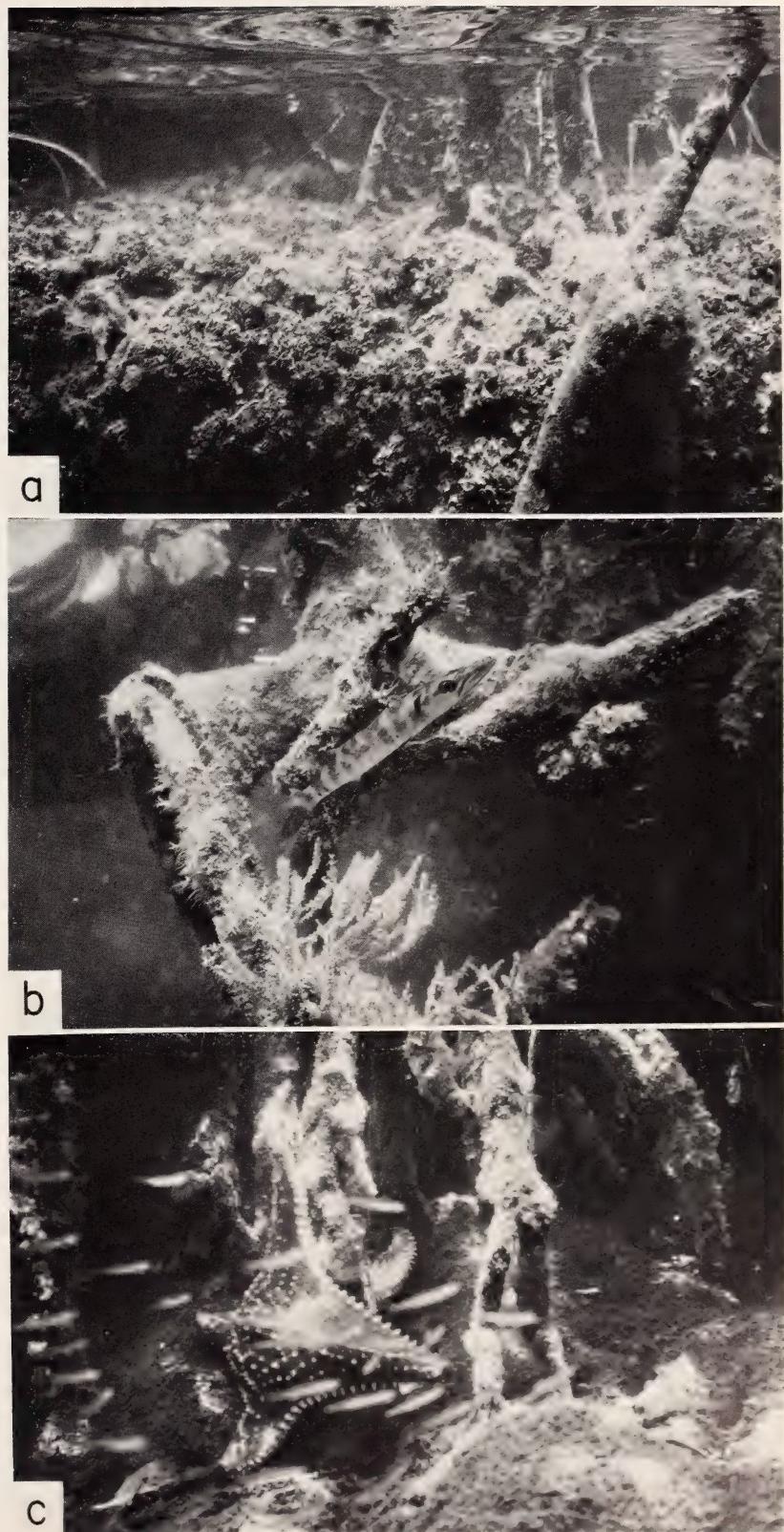


FIGURE 30.—Underwater views of mangrove root system at edge of Twin Cay channel: *a*, mudbank stabilized by rootlets and overgrown by *Halimeda* mat; *b*, juvenile barracuda finding shelter and food among the *Rhizophora* roots; *c*, *Oreaster reticulatus* on mangrove roots penetrating sediment bottom of the channel.

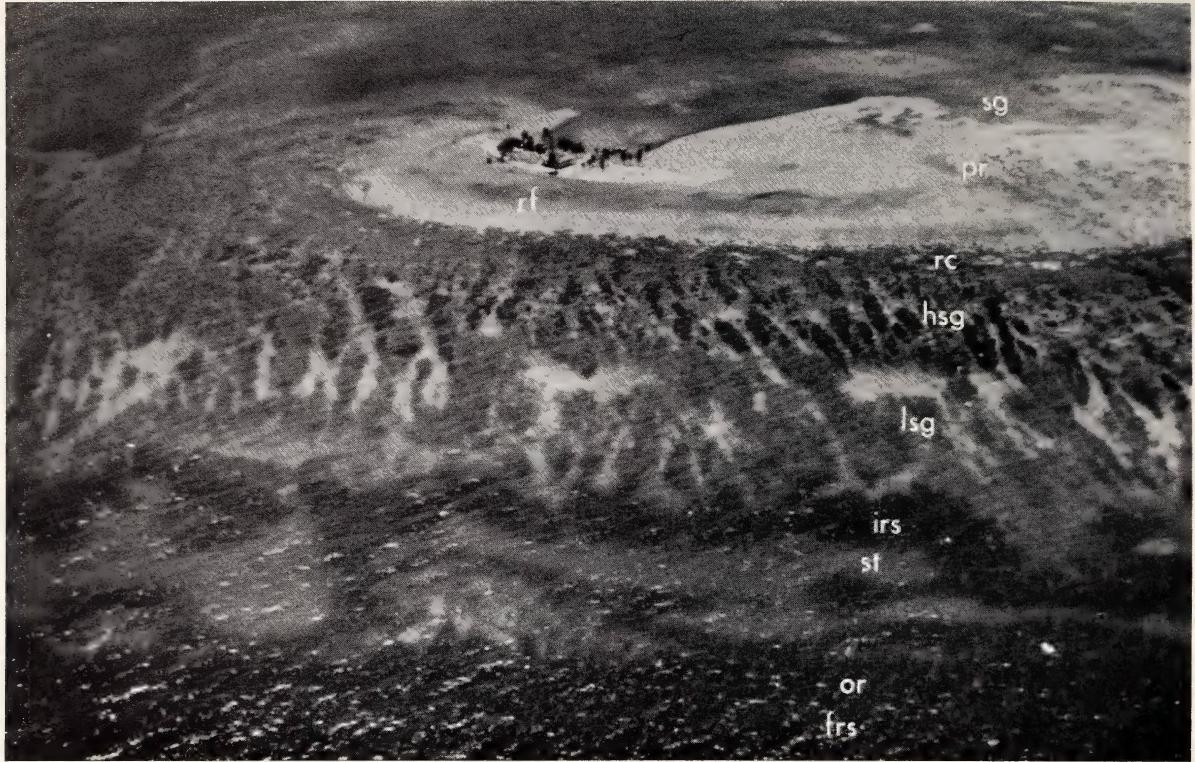
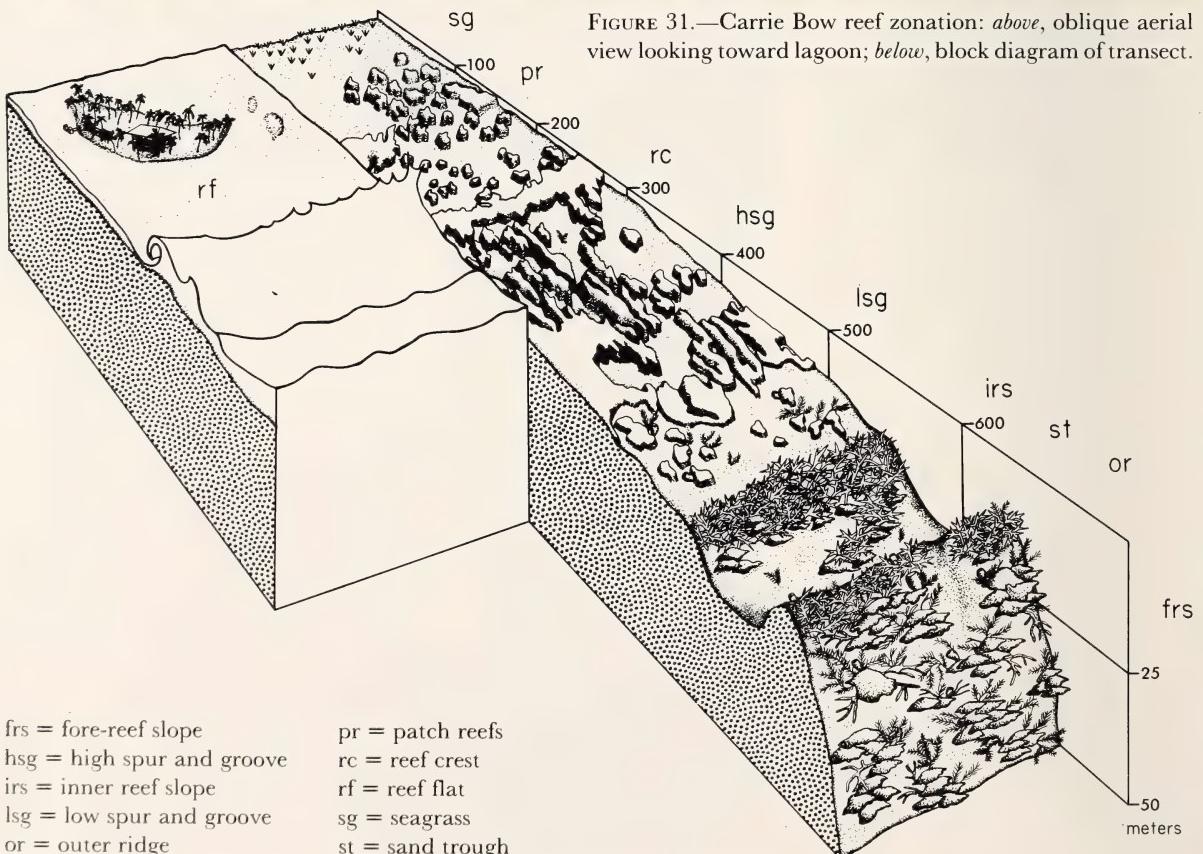


FIGURE 31.—Carrie Bow reef zonation: *above*, oblique aerial view looking toward lagoon; *below*, block diagram of transect.



frs = fore-reef slope

hsg = high spur and groove

irs = inner reef slope

lsg = low spur and groove

or = outer ridge

pr = patch reefs

rc = reef crest

rf = reef flat

sg = seagrass

st = sand trough

gorgonians). Objective evaluation of nonframe-building organisms is essential when comparisons are made between reef biota and nearby lagoon habitats that are not dominated by corals, or only partly dominated by them.

We documented an impressive proliferation of *Acropora cervicornis* in the back-reef and lagoon zones during the four years following the destruction caused by hurricane Fifi in 1974. Our spring 1979 survey indicated that destruction associated with hurricane Greta (September 1978) was mainly the breaking up and lagoonalward transportation of the shallow-water *A. cervicornis*. Few colonies of the fragile branching coral escaped this movement and subsequent burial in the sand and rubble zone as well as in the patch reef zone. Almost all of this coral has been washed out of the rubble and pavement zone (Figure 11). Although many of the living and partly buried fragments will, in time, develop into large colonies, the number of living *A. cervicornis* in shallow water has been drastically reduced. This constant cycle of vigorous development, destruction, and resurgence gives rise to the commonly observed high proportion of *A. cervicornis* rubble in comparison to living *A. cervicornis* in many shallow-reef areas.

Although the branching corals *Acropora palmata* and *A. cervicornis* suffer extensive mechanical damage during hurricanes, the transportation and reestablishment of living fragments are significant factors in the distribution of these corals in the shallow-water environment (Plate 2: center left; Highsmith et al., 1980). Similar observations have been made in Florida (Shinn, 1972; Gilmore and Hall, 1976) and in Jamaica (Tunnicliffe, 1980) where the dispersal of *A. cervicornis* in these reefs was reported to be largely related to asexual reproduction by regeneration of broken and transported branches.

Our observations and those of James and Ginsburg (1978) have documented *Halimeda* as a major contributor to sediment in the Belizean barrier-reef complex. This calcareous green alga forms a major fraction of these sediments, extending from the shallow lagoon down to at least 200

m on the fore-reef slope, well below its living depth range (approximately 100 m). Commonly comprising the dominant component of the extremely coarse fractions (2–4 mm), the readily identifiable calcareous plates of *Halimeda* are more characteristic of reef-derived sediments than are the fragments of any other organisms, including the corals.

The narrow rock pavement that occurs directly shoreward of the reef crest off Carrie Bow Cay (Figure 4) is a characteristic substrate of shallow reef areas that are constantly having their sediment cover swept away by turbulent waters. The dates of  $480 \pm 90$  years and  $534 \pm 90$  years obtained from coral fragments embedded in a pavement off South Water Cay (James et al., 1976) indicate a long period of formation. These dates also support Macintyre's (1977) observation that submarine lithification is most highly developed in reef areas of high agitation and/or slow accumulation, where the substrate is exposed to normal marine conditions for long periods of time.

James and Ginsburg (1978) speculated that a shelf-edge ridge off South Water Cay is a submerged reef similar to the relict shallow-water, Late Holocene reefs described by Macintyre (1967, 1972), Adey et al. (1977), and Lighty et al. (1978). In contrast, Burke (herein) proposed that these ridges are active accumulations of the rapidly growing coral *Acropora cervicornis*. Burke points out that not only is *A. cervicornis* dominant on these ridges, but that the ridges along the barrier reef complex are restricted to areas protected from long-period storm waves by the outlying atolls. The difficulty with which we probed this ridge (an average penetration of 1 m, maximum of 1.5 m) in contrast to the ease of probing through *Acropora cervicornis* at Rhomboid Shoals near Victoria Channel (Macintyre et al., 1977) indicates that this ridge does not have a similar open-frame network. Our earlier observation that *Montastrea annularis* constructs most of the modern framework of the ridge south of our transect also indicates that this shelf-edge ridge is not merely an accumulation of *A. cervicornis*. Core samples of the internal structure are needed to establish the

relative importance of relict and modern framework in the construction of this ridge system.

The reef off Carrie Bow Cay has a species composition and community zonation that is representative of the entire barrier reef system (Burke, herein). The structure of shallow zones of this central province reef, however, is somewhat more similar to that of the discontinuous reefs in

the northern and southern provinces because current flow through South Water and Carrie Bow cuts influences the sediment and coral distribution patterns in the back reef and lagoon. The Carrie Bow Cay fore-reef structures, on the other hand, have a degree of development and flourishing coral communities that are characteristic of the central province.

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# Tides at Carrie Bow Cay, Belize

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## ABSTRACT

The tide at Carrie Bow Cay, Belize, is microtidal (mean range of 15 cm) and is of the mixed semidiurnal type. Comparison with conditions at Key West, Florida, indicates that high and low waters off Carrie Bow occur earlier than at Key West by 45 and 2 minutes, respectively. Because of differences in tidal type and meteorological conditions, corrections for height and time difference applied to the predicted tide at Key West yield only approximate tide predictions for Carrie Bow Cay.

## Introduction

Because the tide in the Caribbean Sea is microtidal, it might be expected to have little influence on the water flow regime. Velocity measurements indicate, on the contrary, that tidal forcing is a major cause of currents in coastal regions of the Caribbean (Roberts et al., 1975). Study of a shallow reef flat and back reef shows that even small tidal fluctuations have strong influence on the distribution and succession of organisms (Glynn, 1973; Rützler, in prep.). This note describes, characterizes, and predicts the tide at Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ), Belize, as a necessary first step in the investigation of flow and water exchange characteristics as well as

intertidal and shallow subtidal communities at this barrier reef location.

**ACKNOWLEDGMENTS.**—Many persons helped to collect the tide data used in this study. We are especially grateful to J. D. Ferraris, Mount Desert Island Biological Laboratory, R. Larson and M. Carpenter, Smithsonian Institution, and J. Greer, R. L. Crout, S. Ferguson, and G. Pickler, University of South Carolina. J. E. Fancher and D. C. Simpson of the National Ocean Survey provided valuable advice on the analytical procedures. L. Kjerfve did the drafting. All computer work was performed on the University of South Carolina IBM 370/168 system. The Belle W. Baruch Institute for Marine Biology and Coastal Research has listed this paper as its Contribution Number 269.

## Measurements, Analyses, and Results

A Benthos 2820 submergible in situ tide recorder, which senses the hydrostatic pressure, was installed below the pier on the west side of Carrie Bow Cay in the barrier reef lagoon. This location is 120 m west of the reef crest, 24 km southeast of Dangriga (Stann Creek). Two major navigation cuts through the barrier reef, less than 1 km away, connect the barrier reef lagoon to the Caribbean Sea. The gauge intake was, on the average, 33 cm off the bottom, 59 cm below water, 153 cm below the top of the cement dock (the local reference datum) and has been operated intermittently since early 1976.

Several 29-day tide records were digitized to hourly intervals and subjected to harmonic anal-

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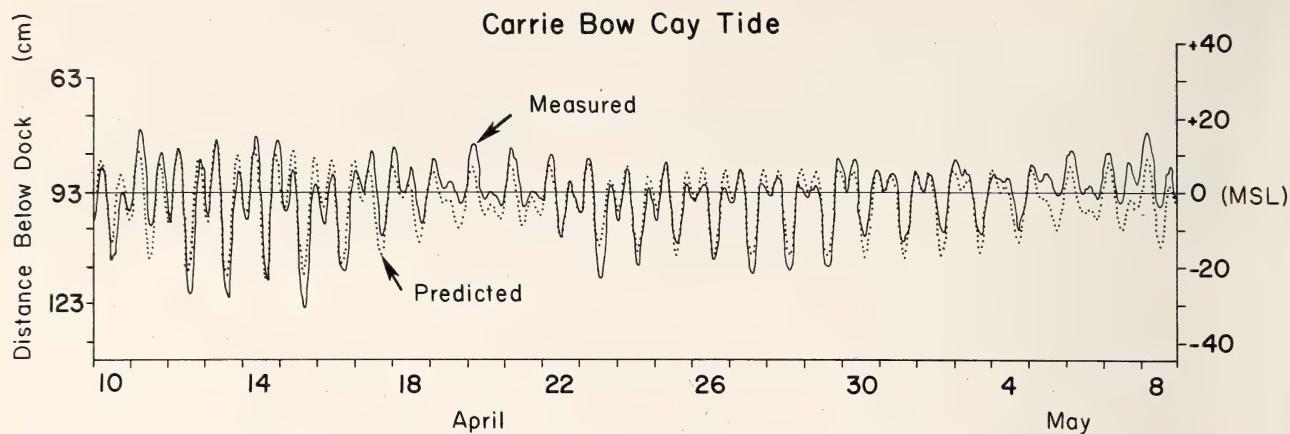


FIGURE 32.—Comparison of measured and computer-predicted tides at Carrie Bow Cay, Belize, 10 April–8 May 1976.

ysis (Schureman, 1940; Dennis and Long, 1971) for the purpose of computing amplitudes and epochs for the 24 major tidal constituents, which correspond to more than 99% of the actual amplitude. The nine constituents with the greatest amplitudes for a typical 29-day series are compared in Table 3 with the same constituents at Key West, Florida. The 24 amplitude and epoch values for Carrie Bow Cay were entered into the National Ocean Survey tide prediction computer program (Pore and Cummings, 1967), which al-

lows monthly prediction of both hourly tidal height values and times and heights of high and low water. Results indicated reasonable agreement between measured and predicted tides for a 29-day test series (Figure 32). The prediction of time of high and low water is in general more successful than reproduction of water elevation.

The 29-day test record, 10 April–8 May 1976, was also tabulated and subjected to high-and-low water analysis on the basis of instructions for Form 2211 (National Ocean Survey, 1974:44-59).

TABLE 3.—Comparison of values for the nine major tidal constituents at Carrie Bow Cay, Belize, and Key West, Florida (symbol in parentheses follows each constituent; columns 1 and 2 computed for Carrie Bow Cay using Program "Harmonic" (Dennis and Long, 1971); columns 3 and 4 supplied by D. Simpson, Predictions Branch, National Ocean Survey; columns 5 and 6 from Defant, 1960: 267)

Tidal constituents	Carrie Bow Cay		Key West		Period (mean solar hour)	Theoretical coefficient ratio ( $M_2 = 100$ )
	Amplitude (cm)	Epoch (°)	Amplitude (cm)	Epoch (°)		
<b>SEMIIDIURNAL COMPONENTS</b>						
Principal lunar ( $M_2$ )	5.7	251	17.8	285	12.42	100.0
Principal solar ( $S_2$ )	3.5	228	5.4	302	12.00	46.6
Larger lunar elliptic ( $N_2$ )	2.5	243	3.5	269	12.66	19.2
Luni-solar ( $K_2$ )	1.0	228	1.5	302	11.97	12.7
Larger lunar evective ( $\nu_2$ )	0.5	244	0.7	271	12.63	3.6
<b>DIURNAL COMPONENTS</b>						
Luni-solar ( $K_1$ )	7.9	185	8.9	282	23.93	58.4
Principal solar ( $P_1$ )	2.6	185	2.9	287	24.07	19.4
Principal lunar ( $O_1$ )	2.5	244	9.2	284	25.82	41.5
Larger lunar elliptic ( $Q_1$ )	0.5	273	2.2	275	26.87	7.9

The pertinent results of this analysis are summarized in Table 4.

## Discussion

The tide at Carrie Bow Cay is microtidal and of the mixed semidiurnal type. Its mean range is 15 cm and its semidiurnal and diurnal amplitudes are of approximately equal importance (Table 3). The form number  $F$ , an amplitude ratio between harmonic constituents, may be used to quantify the tide type (Defant, 1960:306–308). It is defined by  $F = (K_1 + O_1)/(M_2 + S_2)$ , where  $K_1$  is the diurnal luni-solar,  $O_1$  the diurnal principal lunar,  $M_2$  the semidiurnal principal lunar, and  $S_2$  the semidiurnal principal solar component (Table 3). If  $F < 0.25$  the tide is semidiurnal; if  $0.25 < F < 1.50$  the tide is mixed semidiurnal; if  $1.50 \leq F < 3.0$  the tide is mixed diurnal; and  $F \geq 3.0$  the tide is diurnal. The Carrie Bow Cay form number is 1.13 in comparison with 0.75 at Key West, Florida. Although both locations have the same tide type, the diurnal influence is greater at Carrie Bow Cay.

From the amplitude of the various harmonics (Table 3) it is possible to compute additional statistics (Marmer, 1954). With respect to the semidiurnal tidal constituents, the spring tide range is  $2(M_2 + S_2)$  or 18.4 cm and the neap range approximately seven days later of  $2(M_2 - S_2)$  or 4.4 cm. The mean semidiurnal tide is 2.2  $M_2$  or 12.5 cm. With respect to the diurnal constituents, the tropic tide range measures  $2(K_1 + O_1)$  or 20.8 cm, the equatorial range is  $2(K_1 - O_1)$  or 5.4 cm, and the mean diurnal tide is 1.5( $K_1 - O_1$ ) or 15.6 cm. The values above are only approximate as the  $P_1$  and  $N_2$  constituents show values significantly larger than could have been expected from the theoretical coefficient ratio based on the magnitude of the constituents' tide-producing forces (Table 3) at this location. Of course, such discrepancies between the magnitude of the tide-producing force and actual response of the water mass is quite common and is due to basin resonance characteristics.

The diurnal and semidiurnal partial tides are approximately equal; however, the spring-neap-

spring cycle of the semidiurnal tide is 29.5 mean solar days (synodic month) and is related to the phase of the moon. The tropic-equatorial-tropic cycle of the diurnal tide is somewhat shorter, 27.3 mean solar days (sidereal month), and is related to the declination of the moon from the equator. Because of this time difference, several longer cycles are introduced. If the occasional times of high water in  $M_2$ ,  $S_2$ ,  $N_2$ ,  $K_1$ ,  $P_1$ , and  $O_1$  occur simultaneously, the total tide range could be as great as 50 cm. Of course, wind tides are likely to cause extreme sea level changes more so than the astronomical forces.

The epoch or phase relative to the Greenwich meridian yields the following information about the inequality of the timing of highs and lows in the component tides (Marmer, 1949). If epochs are expressed in degrees, the difference  $D = |M_2^0 - (K_1^0 + O_1^0)|$  indicates whether tidal inequality is entirely in the high waters ( $D \approx 0^\circ$ ), is equally great in the high and low waters ( $D \approx 90^\circ$ ), or is entirely in the low waters ( $D \approx 180^\circ$ ). If  $D$  is greater than  $180^\circ$ , its value is subtracted from  $360^\circ$ . For Carrie Bow Cay, the  $D$  value of  $120^\circ$  indicates inequality in both high and low waters, which is especially pronounced in the low water elevations (refer to Figure 32). This so-called diurnal inequality on the average measures 5.6 cm between low waters and 2.4 cm between high waters (Table 4).

The epoch also yields information about the phase age and the diurnal age. The phase age

TABLE 4.—Tide statistics for Carrie Bow Cay, corrected for the longitude of the moon's node and changes in the declination of the sun, based on computations using National Ocean Survey Form 2211 for 10 April–8 May 1976 (refer to Figure 32)

Tide datum (mean low water) <sup>1</sup>	0 cm
Mean range (Mn)	15.0 cm
Mean tide level (MTL) <sup>2</sup>	7.5 cm
Diurnal high water inequality (DHQ)	2.4 cm
Diurnal low water inequality (DLQ)	5.6 cm
Greenwich lunital high water interval	2.14 h
Greenwich lunital low water interval	8.44 h

<sup>1</sup> 101 cm below local reference datum.

<sup>2</sup> Marked "0" on Figure 32, right hand scale.

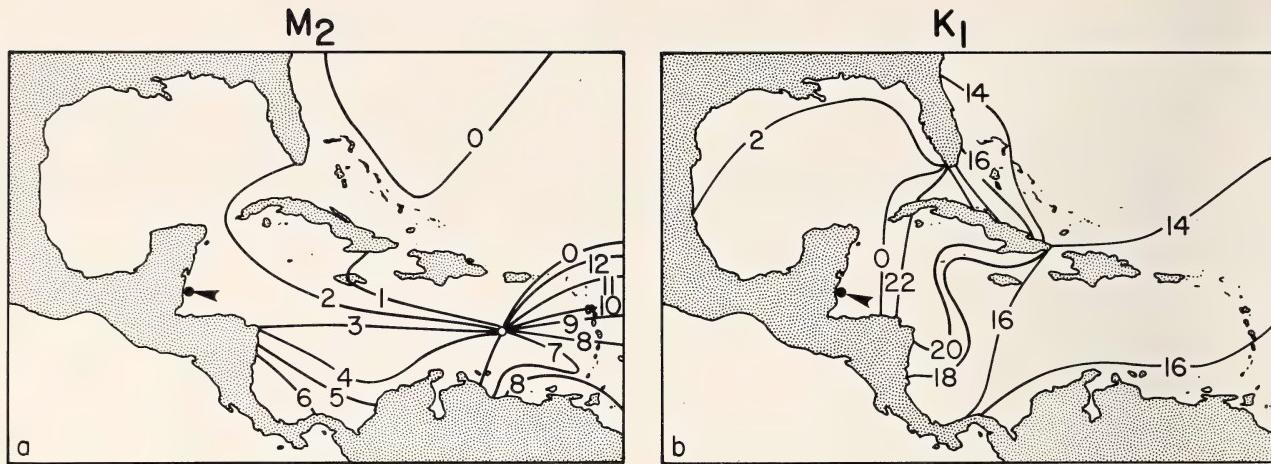


FIGURE 33.—Co-tidal lines of the predominant tides for the Caribbean Sea (after Defant, 1960); tide regression indicated by relative arrival time of high or low water, expressed in lunar hours: *a*, semidiurnal tide,  $M_2$  constituent, progresses along the Belizean coast from north to south; *b*, diurnal tide,  $K_1$  constituent, progresses along the Belizean coast from south to north. (Carrie Bow Cay indicated by arrow).

refers to the semidiurnal tide and is the lag of the spring tide relative to full or new moon. The phase age is computed as  $0.98(S_2^0 - M_2^0)$  and equals -22 hours for Carrie Bow Cay, which indicates that spring tide leads the new and full moon by 22 hours. The diurnal age, on the other hand, is a measure of the timing of tropic tide relative to maximum declination of the moon. It is computed as  $0.91(K_1^0 - O_1^0)$  and is 0 hours for Carrie Bow Cay, indicating a maximum diurnal tide range at the time of maximum lunar declination.

Figure 33, which shows the main Caribbean semidiurnal ( $M_2$ ) and diurnal ( $K_1$ ) amphidromic systems (Defant, 1960) indicates that the  $M_2$  tide progresses from north to south along the Belizean barrier reef, whereas the  $K_1$  tide progresses in the opposite direction, from south to north, along the reef crest.

Because it is inconvenient, though possible, to publish tidal predictions for Carrie Bow Cay, we instead computed correction factors and applied

them to predicted tides for Key West, Florida, a National Ocean Survey reference gauge for which daily predictions are published. The Greenwich lunital intervals at Key West are 2.89 hours for high water (HW) and 8.48 hours for low water (LW) (D. Simpson, pers. comm.). Comparison of these figures with the lunital intervals for Carrie Bow (Table 4) indicates that on the average HW at Carrie Bow Cay leads HW at Key West by 45 minutes, and LW at Carrie Bow Cay leads LW at Key West by 2 minutes. Using the predicted tides for Key West for April and May 1976, we also found that HW at Carrie Bow Cay is 23 cm below HW at Key West and that LW at Carrie Bow Cay is 4 cm above LW at Key West on the average. However, because Carrie Bow Cay and Key West can be expected to experience different meteorological and oceanographic conditions at given times, the resulting tide predictions for Carrie Bow Cay now and then will deviate significantly from actual tide variations.

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# Water Currents Adjacent to Carrie Bow Cay, Belize

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## ABSTRACT

Tide, wind, and waves significantly influence the water currents off Belize, as indicated by continuous current-meter measurements at four locations in or behind the barrier reef at Carrie Bow Cay. Tidal currents reaching speeds of up to  $40 \text{ cm s}^{-1}$  are dominant in the major reef entrances. In the lagoon behind the reef crest, the water is primarily wind driven, without an obvious tidal signature, and reaches maximum speeds of  $33 \text{ cm s}^{-1}$ . On the leeward side of Carrie Bow Cay a slow wave drift accounts for the maximum  $6 \text{ cm s}^{-1}$  flow. During the late part of the study, a tropical depression forming just east of Carrie Bow Cay caused an abnormally high mean tide that increased the flow of water into the lagoon.

## Introduction

Coral reef ecosystems are controlled by the complex interaction of biological, chemical, geological, and physical parameters (Odum and Odum, 1955), of which the least understood are probably the physical forces—waves, winds, tides (see for example Macintyre et al., 1974). Early studies of the physical oceanography of reefs focused primarily on Pacific atolls (Munk and Sargent, 1948; von Arx, 1948) and paid considerably less attention to coral reefs in the Caribbean.

Although recent investigations have increasingly shifted to the Caribbean, mainly because of proximity for American workers, physical oceanographic investigations of the well-developed barrier reef of Belize are only beginning. Previous physical research in this area was concerned with waves and wave-related processes (Roberts, 1974; Roberts et al., 1975; Shinn, 1963; Storr, 1964; Wilson et al., 1973), so that the interaction of tides with other physical processes has received little attention. Recent work on Grand Cayman (Roberts et al., 1977) suggests strong tidal influence on physical processes within the shallow fore-reef region. Because the tide in the Caribbean is microtidal and of mixed semidiurnal type (Kjerfve et al., herein), it might be expected to have considerably less influence on the reef system than wind-driven currents and waves. Our study around Carrie Bow Cay indicates that just the opposite may be true—that is, tidal processes may play a major role in controlling the water movements within the reef system.

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## Site, Measurements, and Analysis

The barrier reef off Belize, which extends in a north-south direction for over 200 km, is separated from the mainland by a lagoon that is 10–25 km wide and 5–20 m deep. The study area, Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ), a small, sandy cay approximately 120 m long and 30 m wide, lies 100 m west of a well-developed section of the barrier reef crest (Figures 34, 40). Two large cuts, 12 m deep and approximately 1 and 2 km wide, respectively, separate the Carrie Bow reef section from Tobacco Reef to the north and Gladden Cay Reef to the south (Figure 2). Carrie Bow receives steady northeasterly trade winds and has a mixed semidiurnal tide with a mean range of 15 cm.

Current, tide, wind, and atmospheric pressure were measured in June 1978. A Bendix Q-15 recording current meter suspended from a

moored boat was monitored at five locations (Figure 34) in the vicinity of Carrie Bow Cay for time periods ranging from 17 to 74 hours. At each location the Q-15 was positioned at mid-depth. At location L1 it was placed in the lagoon 125 m WSW of the island, where the total water depth was 4 m (duration, 24 hours); at locations L2 and L4 it was placed in South Water Cut above a large, flat sand plain in depths of 11 m (duration, 43 and 44 hours, respectively); at location L4 it was in Carrie Bow Cut above a 10 m deep sand channel (duration, 74 hours); and at location L5 it was in the lagoon 150 m W of the main study transect (Rützler and Macintyre, herein), where total water depth was 3 m (duration, 17 hours).

Each record of current speed and direction was digitized at 10 min intervals, resolved into E-W and N-S components, and then averaged vectorially to obtain resultant hourly speeds and directions. The time-series plots of the data obtained in the South Water Cut and Carrie Bow Cut are shown in Figures 35 and 36. Current records for stations L1 and L5 are presented as progressive vector diagrams in Figure 37.

A Benthos 2820 submergible recording tide gauge was installed below the dock on Carrie Bow Cay to obtain the complete tidal record during the study (Figure 38). Wind speed and direction were read on a cup anemometer with vane every hour on the hour; readings were averaged by eye for 30 s to smooth high-frequency noise. The wind data are plotted on a frequency isopleth in Figure 39. The atmospheric pressure was measured using a Weather-Measure B211 recording microbarograph.

## Results and Discussion

Northeasterly winds with speeds of  $4\text{--}5 \text{ m s}^{-1}$  were most frequent during the study period. These conditions seem to prevail during 70% of the year (Rützler and Ferraris, herein). Sustained winds did not exceed  $9 \text{ m s}^{-1}$  and the wind direction varied little from northeast. During the latter part of the study (16–20 June), the average wind speed increased slightly, to  $6.5 \text{ m s}^{-1}$ , and water levels became abnormally high. The in-

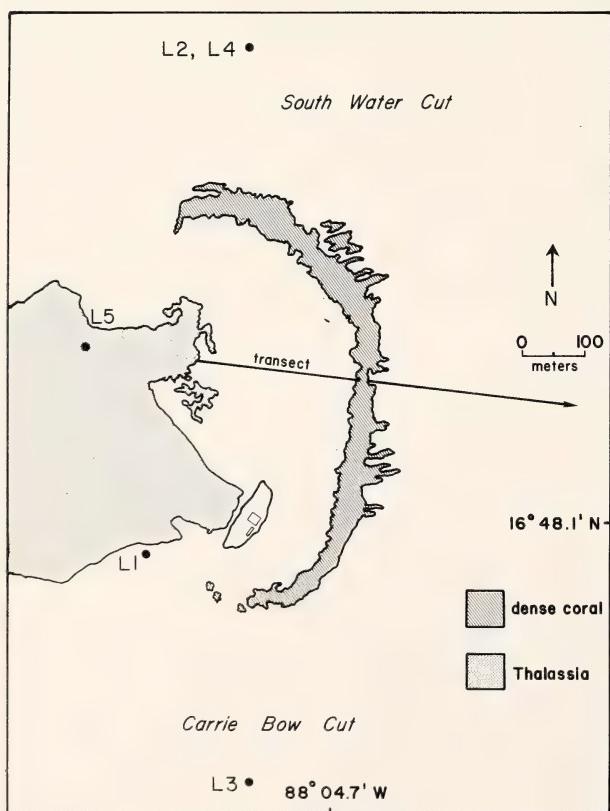


FIGURE 34.—Location of current meter stations around Carrie Bow Cay.

### South Water Cut (L2, L4) Current

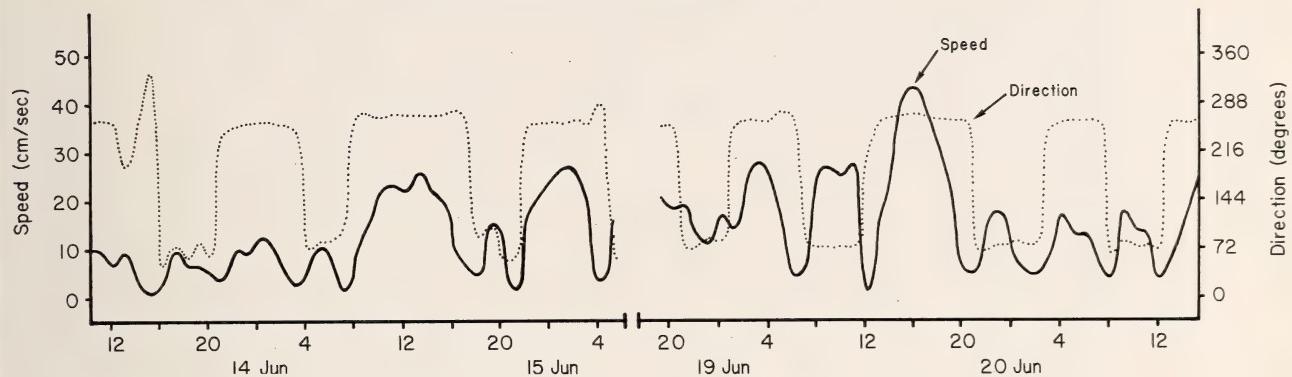


FIGURE 35.—Time-series of current speed and direction in South Water Cut at current meter locations L2 and L4, using vectorially averaged hourly values.

### Carrie Bow Cut (L3) Current

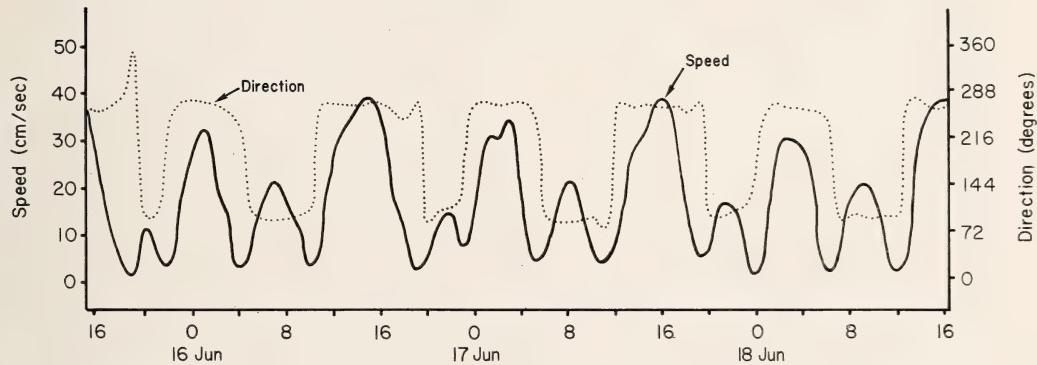


FIGURE 36.—Time-series of current speed and direction in Carrie Bow Cut at current meter Location L3, using vectorially averaged hourly values.

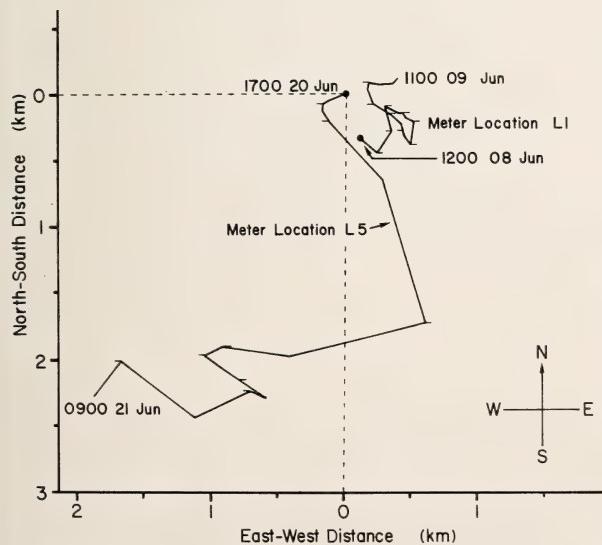


FIGURE 37.—Progressive vector diagram of currents at current meter locations L1 and L5, using vectorially averaged hourly values.

creased wind speed and water level were probably related to a tropical depression that was developing east of Glover's Reef. The atmospheric pressure showed a net drop of 6 mb from 15 to 20 June.

The predominant flow feature observed in the major reef cuts was a strong tidal periodicity with flood currents greatly exceeding the ebb currents. Maximum current velocities in South Water Cut were  $26 \text{ cm s}^{-1}$  and  $43 \text{ cm s}^{-1}$  during the first (L2) and second (L4) study periods, respectively. In

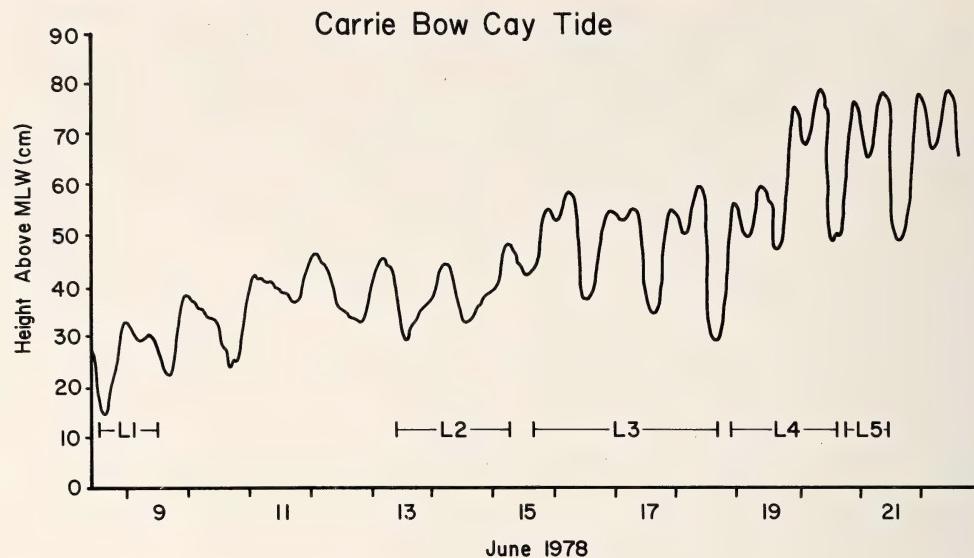


FIGURE 38.—Measured tide at Carrie Bow Cay dock, 8–22 June 1978; numbered segments indicate water elevations when Q-15 current meter was in operation at locations L1–L5.

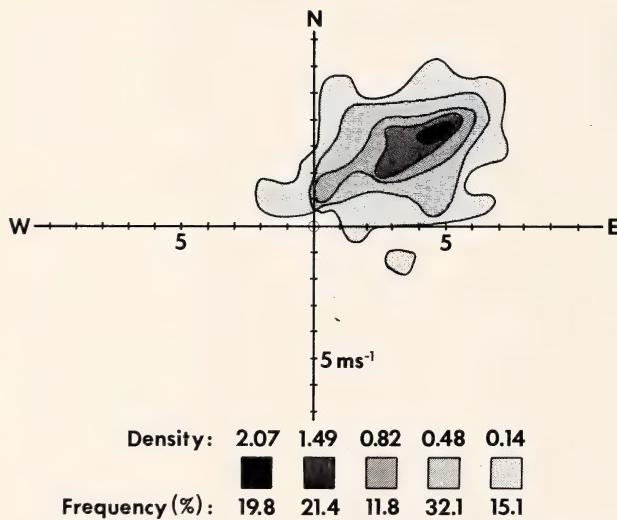


FIGURE 39.—Frequency isopleth diagram (modified from Seppälä, 1977) of 312 hourly recordings of wind data at Carrie Bow Cay, Belize, 8–22 June 1978, indicating density of wind observations (in observations per  $m s^{-1}$  and  $15^\circ$  segments) and percentage of frequency corresponding to a given direction.

Carrie Bow Cut, observed hourly peak velocities measured  $40 \text{ cm s}^{-1}$ . Directional changes during each half tide (rising or falling) were negligible in both South Water and Carrie Bow cuts. In South Water Cut the average resultant direction for

inflow was toward  $260^\circ$ , and for outflow toward  $70^\circ$ . In Carrie Bow Cut the flood flow was toward  $275^\circ$  and the ebb flow toward  $105^\circ$ . The predominance of the flooding tide over the ebb during the study period indicates a slow, continual infilling of the lagoon, which is also indicated by data for the mean increase of the tide level (Figure 38). The tidal pattern was due to the stationary tropical depression to the east of Carrie Bow, which had strengthened the northeast trade winds.

Current patterns observed at lagoon stations L1 and L5 are shown in Figure 39 on a progressive vector diagram. Neither location exhibited the obvious tidal activity that had occurred at stations L2, L3, and L4. Meter location L1 showed weak water movement and little effects of tidal or wind forcing. Hourly averaged currents at L1 did not exceed  $6 \text{ cm s}^{-1}$  and were generally on the order of  $2 \text{ cm s}^{-1}$ . This location, being on the lee side of the island, was shaded from direct wind influence. The net flow direction to the northeast at L1 suggests that the current was due to wave drift. The wave crests that propagated into Carrie Bow Cut were greatly refracted by the reef crest and entered the Carrie Bow lagoon from the southwest, as indicated by waves break-

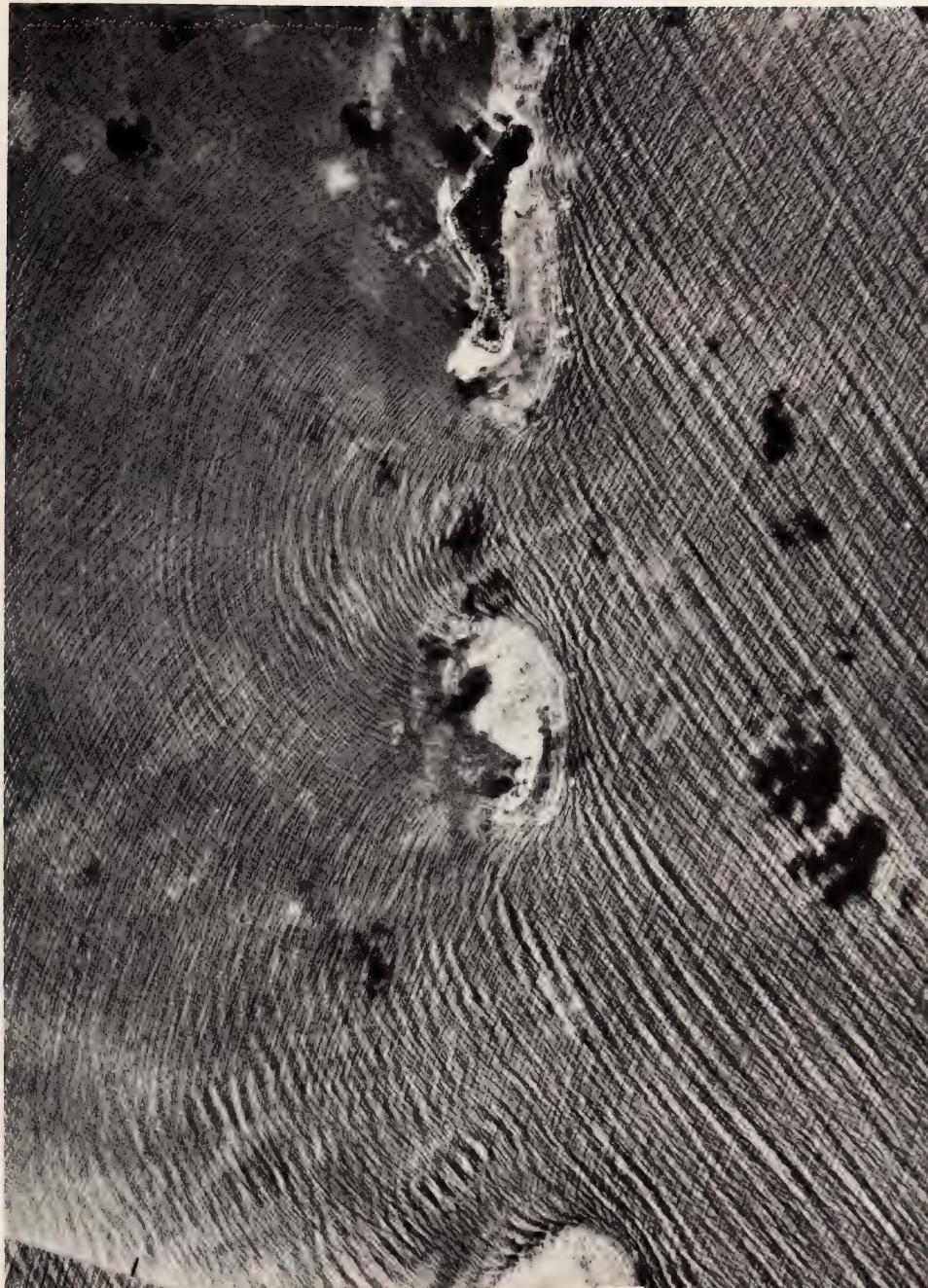


FIGURE 40.—Vertical high altitude aerial photograph of Carrie Bow Cay (center) showing wave refraction patterns; island to the north (top) is South Water Cay, sand bank to the south (bottom) is Curlew Bank (picture area =  $2.5 \times 3.5$  km).

ing on the lee side of the island and refraction patterns on aerial photographs (Figure 40).

Although higher water levels and increased wind speeds due to the developing tropical depression were atypical conditions for station L5,

these conditions probably did not alter the typical flow patterns there, but merely modulated their intensity. Maximum hourly velocities at L5 were  $33 \text{ cm s}^{-1}$ , with a net flow direction due southwest, varying almost  $180^\circ$  from that at L1. The current

at L5 did not have the strong tidal signature evident in the major reef cuts. Rather, water was being driven across the reef crest and into the lagoon by the northeasterly trade winds. While the higher than usual water levels and increased wind speeds tended to move more water across the crest than usual, the current at L5 appeared to be primarily wind-driven.

### Conclusions

Current flow through the major reef cuts bordering Carrie Bow Cay appears to be tidally

dominated despite a small tidal range. Measurements within the cuts showed a predominance of flooding over ebbing currents that was related to increased northeasterly winds associated with the development of a tropical depression to the east of the island. Depending on location, net currents inside the lagoon may be wave-driven, wind-driven, or both. Current records from this area lack the clear tidal signature that was observed in Carrie Bow and South Water cuts. Because our study was conducted in the early summer, however, caution must be exercised in extrapolating the results to other seasons.

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# Water Exchange across the Reef Crest at Carrie Bow Cay, Belize

Björn Kjerfve

## ABSTRACT

Water movement across the reef crest off Carrie Bow Cay, Belize, is affected by at least five microgrooves, 2–4 m wide and 1–3 m deep, cutting across the reef crest and connecting the shallow reef lagoon and the open Caribbean Sea. The currents in these microgrooves flow into the lagoon during rising tides and out to sea during falling tide. Over one or more tidal cycles, however, net flow inside the microgrooves is directed toward the ocean and along the remainder of the reef crest it is directed toward the lagoon owing to water being pumped over the crest by breaking waves.

## Introduction

Few environments are as hazardous or as difficult to sample as the reef crest on an exposed coast. Breaking waves that pound the outside edge of the reef dissipate vast quantities of energy, and cause water to be pumped across the crest. In addition, the water flow over the reef is typically influenced by tidal currents, hydraulic head differences (Tait, 1972), and persistent  $4\text{--}8 \text{ m s}^{-1}$ , trade winds. Few studies have examined this complex of water motions.

Munk and Sargent (1948) noted that “surge channels,” cutting across the reef crest and reef flat on the windward side of Pacific atolls, are tuned to the average wave characteristics and

play an important role in the dissipation of wave energy. Although Roberts et al. (1975) found no evidence of surge channels in exposed fringing reefs around Grand Cayman and Barbados, a section of the Belizean barrier reef at Carrie Bow Cay in the western Caribbean ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ) has at least five channels cutting across the reef crest. Because of their small size and other characteristics that differ from the atoll surge channels, the Carrie Bow channels are called “microgrooves” in the following description of their role in the water exchange across the reef crest.

**ACKNOWLEDGMENTS.**—For help with the collection of field data in 1977 and 1978 I am especially indebted to J. B. Atkins, F. M. Drescher, J. E. Greer, and J. A. Proehl, University of South Carolina; L. Greczy, Louisiana State University; and to L. Kjerfve, J. Stallings, United States Geological Survey, and D. Middaugh, Environmental Protection Agency, donated Rhodamine dye and practice golf balls, respectively, for numerous qualitative flow experiments. The Belle W. Baruch Institute for Marine Biology and Coastal Research has listed this paper as its contribution Number 271.

## Results

**MICROGROOVES.**—The Carrie Bow section of the barrier reef lies just off the south end of Tobacco Reef. It is separated from South Water Cay by a cut, 800 m wide and 12 m deep. The reef crest forms a half-ellipse 1000 m long (Figure 41) that consists of dense growths of *Acropora*

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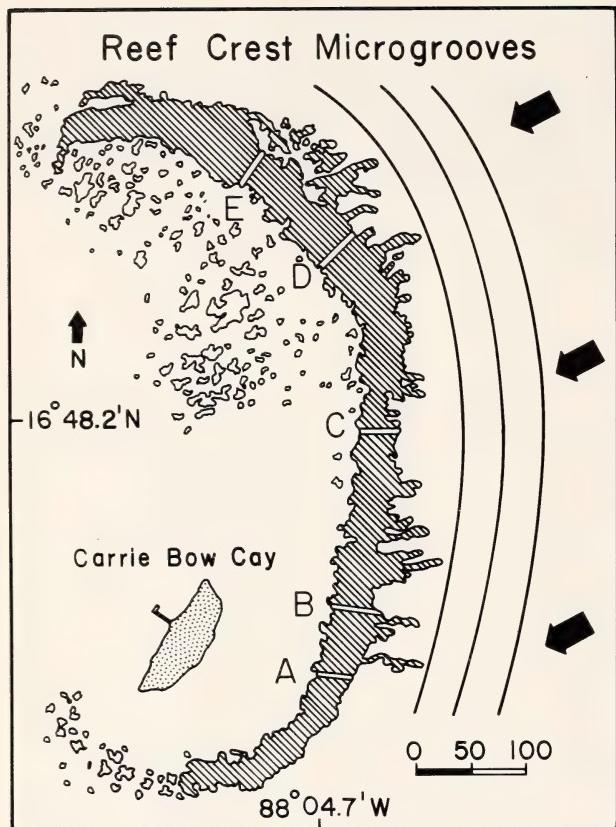


FIGURE 41.—Schematic representation of the Carrie Bow Cay reef crest, indicating location of five microgrooves (A–E), refraction of typical wave crests before breaking, (curved lines) and direction of predominant trade winds and deep water waves (arrows). (Scale in m.)

*palmata*, *Millepora complanata*, *Agaricia agaricites*, *Porites astreoides*, and other corals. The elevation at the crest coincides approximately with the mean low water level. The crest measures 20–35 m across from a 1 m deep sand-filled moat on its lagoon side to another 4 m deep sand moat on its seaward side.

The lagoonward edge of the reef crest is irregularly indented and gives the impression that numerous channels open into the ocean. Most of these cuts, however, extend only part of the way across the crest, except for five locations (Figure 41) where the channels traverse the crest and thus make it possible for a swimmer to reach the fore reef even during moderate wave conditions. These small passages are the microgrooves (2–4

m wide and 1–3 m deep) that wind their way across the crest; they typically exhibit a constricted area somewhere between the lagoon and ocean where the water becomes significantly shallow compared with the rest of the microgroove. The bottom of the microgrooves consists of poorly sorted carbonate sand and large amounts of broken coral branches and rubble. Large numbers of schooling fish appear to be associated with the microgrooves. Microgroove E (Figure 41) across the well-developed northern section of the reef at Carrie Bow Cay is by far the deepest and widest one.

The microgrooves differ from atoll surge channels (Munk and Sargent, 1948) in several ways: they are shallower and narrower; they extend across the reef crest with several bends and branchings; they usually do not align with a fore-reef groove; they appear less well tuned to the predominant waves. These differences, however, may all be due to the calmer wave climate in the Caribbean. Whereas the trade-wind-generated waves on Bikini Atoll are 2.0–2.5 m high with steady 7–9 s periods, the Carrie Bow reef usually experiences 1.0–1.5 m, 4–5 s waves with a great variability over time.

**WATER EXCHANGE.**—As wave crests progress toward a reef they shoal and refract. Before waves reach the breaking point, refraction causes their crests to become almost parallel to the outer reef edge (Figure 41). When a wave breaks, water is pumped across the reef crest (Shinn, 1963) and some water surges back before the arrival of the next breaker. The available wave energy is transformed into kinetic energy and is dissipated, and thus helps to maintain a superelevated water level at the breaking point, in contrast to the still-water levels of the lagoon (Munk and Sargent, 1948). This reef set-up may be as much as 20% of the incident wave height (Tait, 1972). If the waves are high, the set-up can drive over the reef crest a steady net inflow, which becomes superimposed on the more or less symmetrical, oscillatory pumping and return-surge action due to breakers. Because of refraction, waves usually traverse the barrier perpendicular to the local crest axis and

along the mean direction of the microgrooves. As in the case of atoll surge channels, this pattern suggests a close relationship between microgrooves and wave action.

Qualitative features of the reef-crest water exchange were assessed by means of current-meter measurements and dye drops during March 1977 and June 1978. A Bendix B-10 impeller-type, ducted, bidirectional current meter was placed at approximately middepth in microgrooves A, B, and C, as well as in two locations on the reef crest between microgrooves B and C. At each location two 25 h time series were obtained via a 200 m cable connecting the sensor and a shore-based read-out unit and recorder. The signal was subjected to a 2.5 s RC low-pass filter, and was then read every 5 s for 3 min on the hour every hour. Statistically significant hourly mean values based on 36 readings were plotted versus time, and compared with the tide for the same period. The resulting plot for microgroove B is shown in Figure 42, that for the reef crest in Figure 43. In

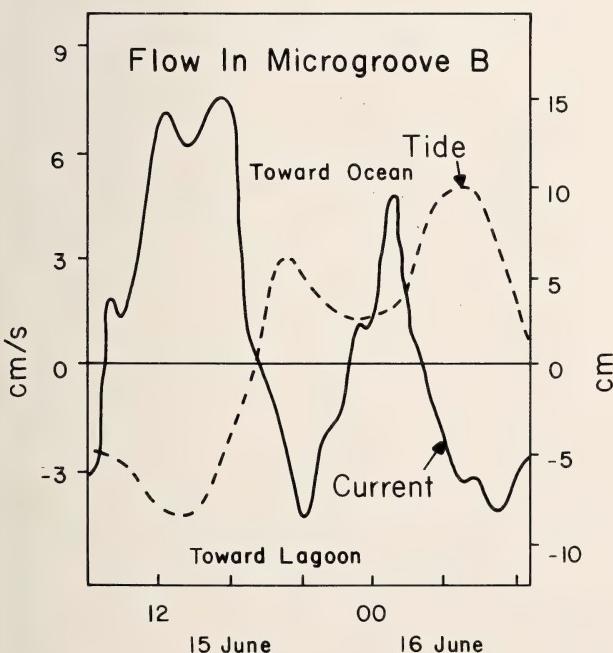


FIGURE 42.—A 25 hour time series of low-pass filtered current in microgroove B, 15–16 June 1978, with simultaneous tide record at the Carrie Bow dock (positive current = lagoonward flow, negative current = oceanward flow).

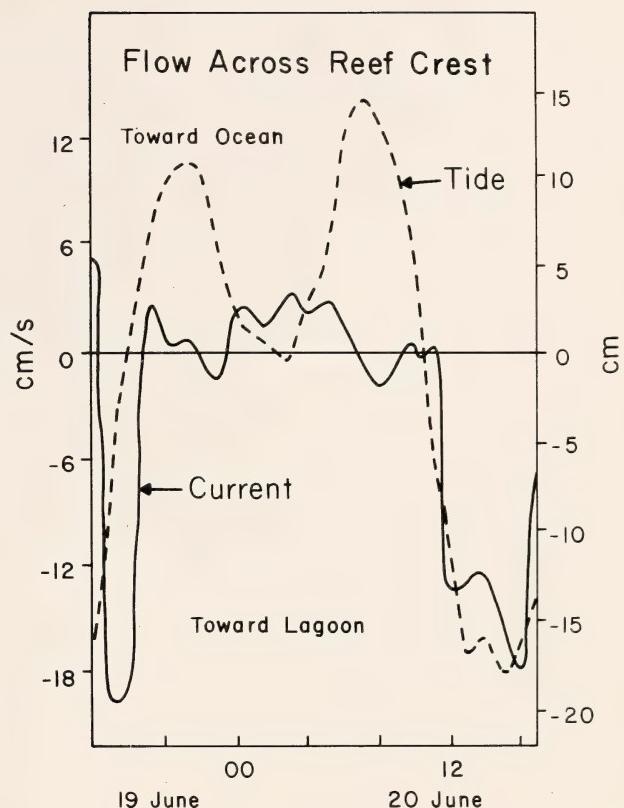


FIGURE 43.—A 25 hour time series of the low-pass filtered current on top of the reef crest between microgrooves B and C, 19–20 June 1978, with simultaneous tide record at the Carrie Bow dock (positive current = lagoonward flow, negative current = oceanward flow).

addition, Rhodamine B dye was released at approximately 50 locations along the Carrie Bow section of the barrier, in front of the reef, in the lagoon, on top of the crest, and in all microgrooves during both falling and rising tides. In addition, water movement was traced by means of 200 plastic practice golf balls released at several locations oceanward of the reef and observed as they crossed the reef crest; these were subsequently collected.

### Conclusions

Although these experiments yielded primarily qualitative results, several generalizations can be made. Currents in microgrooves as well as on top of the reef crest varied on at least two time scales:

wave and tide frequencies. The wave-induced motions were largely oscillatory and perpendicular (back and forth, up and down) to the crest with typical instantaneous microgroove speeds of  $10\text{--}60 \text{ cm s}^{-1}$ . The hourly means, however, reflect the tidal forcing and were typically  $1\text{--}20 \text{ cm s}^{-1}$  m in the microgrooves, directed oceanward (negative) during falling tide and lagoonward (positive) during rising tide. The current on top of the reef crest behaved similarly but exhibited a much greater variation than it did in the microgrooves.

Both microgroove and reef-top currents clearly display the tidal signature. When averaged over a 25-hour period (2 semidiurnal or 1 diurnal cycle), however, the microgrooves showed a net oceanward flow, whereas the water on top of the crest is directed toward the lagoon (Figure 43).

Dye experiments during the falling tide indicated a jet-like flow from the microgrooves into the fore reef region. Once outside the reef, some of this water is transported southward with the longshore current. Most of the dye seemed to return via wave-pumping over the reef crest both up- and down-stream of the microgroove exits, thus setting up a series of circulation cells along the outer reef edge. The currents are much more vigorous at microgrooves C, D, and E compared with B and A. Instantaneous and time-averaged values were greater here because in this region the incident waves have been subjected to a minimum of refraction.

The features described thus far reflect trade wind conditions estimated to occur 70 percent of the time (Rützler and Ferraris, herein). During minor storm events and other times of high wave activity, however, both reef crest and microgroove net currents flow toward the lagoon and do not display any tidal influence. At these times, the wave set-up is probably sufficiently greater to dominate any tidal influence by exceeding any differences in tidal hydraulic head. Water then leaves the shallow Carrie Bow lagoon both at the north and south of the island.

Although Hernandez-Avila et al. (1977) found that during storms, coral rubble was transported from the deep fore reef to form coral boulder ramparts along the south coast of Grand Cayman, elsewhere in the Caribbean sand-sized material appears to be slowly transported away from the reef crest. These observations are not contradictory. In view of the measured ocean-directed net flow at Carrie Bow Cay, it can be assumed that the microgrooves act as a passway for sediment from the lagoon and reef crest during typical conditions. When a storm strikes, however, the wave drift is directed up the fore reef and the forces are great enough to transport boulders toward and over the reef. The rubble rampart that makes up the SE reef crest of Carrie Bow Cay (Rützler and Macintyre, herein:9) undoubtedly owes its existence to wave transport during heavy storms.

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# Geology and Sediment Accumulation Rates at Carrie Bow Cay, Belize

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## ABSTRACT

A 24 km long transect of cores consisting of four rotary drill cores and seven vibrocores was drilled in a line extending from the seaward side of the reef crest at Carrie Bow Cay to the mainland at a point between Sittee Point and the town of Stann Creek. Two of the four rotary cores were drilled seaward of the reef crest, one through a spur to a depth of 7.6 m and the other into the adjacent groove to a depth of 18.3 m. The two cores show no evidence that the spur and groove system was erosional in origin; rather, they demonstrate that it was constructional. Submarine cementation, chiefly in the form of fine-grained high-magnesium calcite, was found mainly in cemented internal sediment in both cores drilled seaward of the reef crest.

Two other rotary cores were drilled landward of the reef crest. One was drilled on the reef flat to a depth of 8.8 m, and the other was drilled on the southwest tip of Carrie Bow Cay to a depth of 17.7 m. Both cores encountered essentially uncemented carbonate reef sands with some coral rubble. Of the four rotary cores, only the Carrie Bow Cay core encountered Pleistocene bedrock. Radiocarbon dating of a large head of *Siderastrea siderea*, growing on bedrock from the Carrie Bow Cay core at a depth of 15.04 m below sea level, gave an age of  $6960 \pm 110$  years. The leached calcitic coralline bedrock, at a depth of 15.7 m below sea level in the Carrie Bow Cay core, contained root marks, and iron staining indicative of subaerial exposure.

Five of the seven vibrocores, with sediment recoveries ranging from 1.6 to 5 m, contained peat. Generally, the peat was located near the bottom of the cores, and in the four most landward cores the peat overlay clay, silt, quartz sand, and in some a few quartzite pebbles. The peats are interpreted to record flooding of the coastal plain during the last transgression. Radiocarbon dates of peats overlying terrigenous sediments range from  $6804 \pm 150$  to  $8808 \pm 600$  years.

## Introduction

This paper reports the results of rotary rock coring on and around Carrie Bow Cay and describes a transect of seven sediment vibrocores drilled in a line from Carrie Bow Cay to the mainland, 24 km to the west.

Carrie Bow Cay, literally within a stone's throw of the reef at  $16^{\circ}48'10''N$ ,  $88^{\circ}04'45''W$ , is situated between two tidal passes that cut through an otherwise continuous reef flat (Figure 2). Tidal passes through the Belize barrier reef are rare, but wherever they occur, they are adjacent to islands situated near the edge of the reef tract. Carrie Bow, like other islands on the shelf south of the Belize River, is a Holocene sedimentary accumulation. Although there are extensive exposures of Pleistocene limestones at the northern limits of the Belizean barrier reef complex, notably Ambergris Cay, nowhere within Belizean waters south of the Belize River do Pleistocene or older limestones extend to or above sea level to form an island, as is common in other coral reef areas of the Caribbean. Sediments, vegetation,

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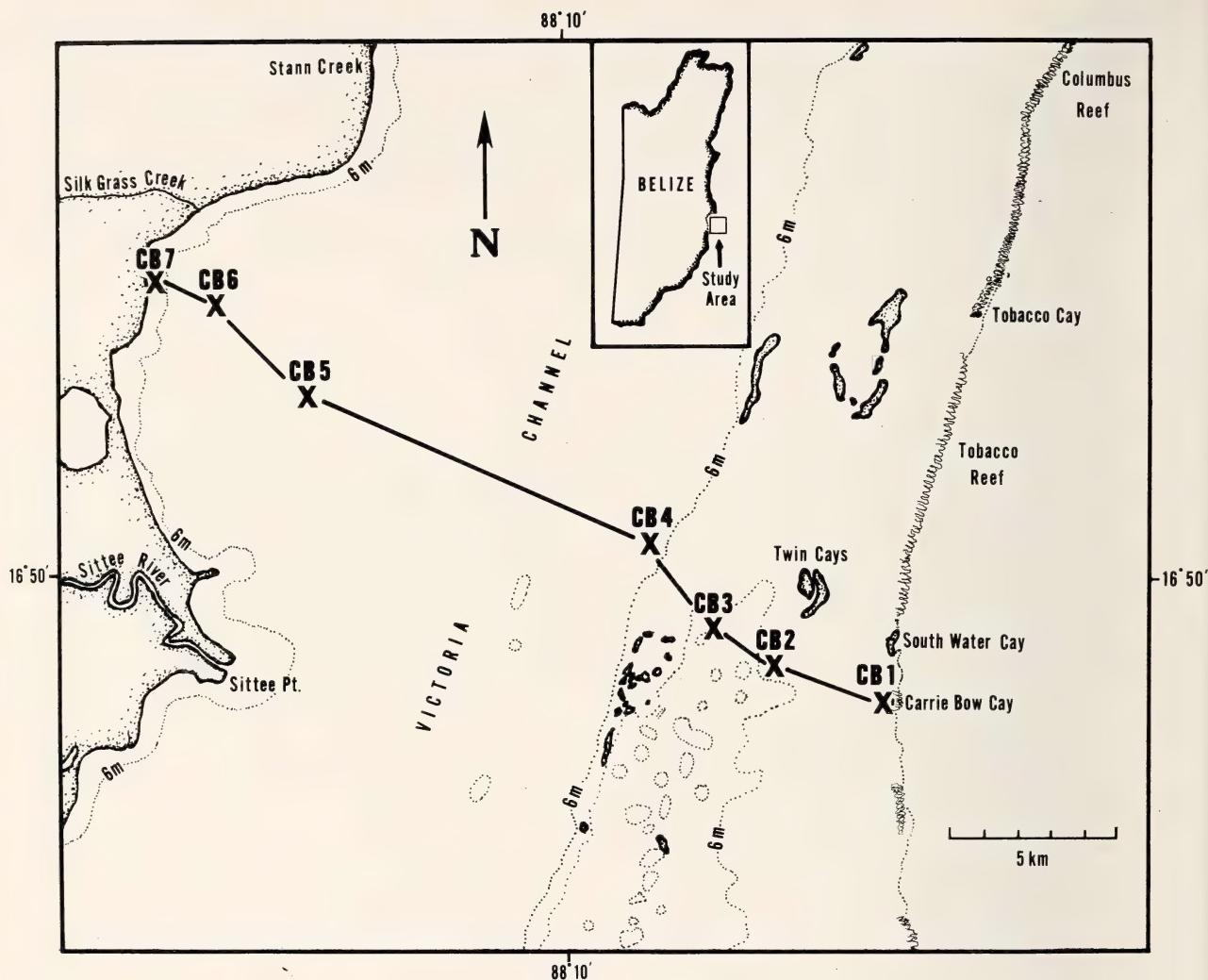


FIGURE 44.—Map of Carrie Bow Cay study area, Belize, showing transect of sediment vibrocores (CB1–CB7).

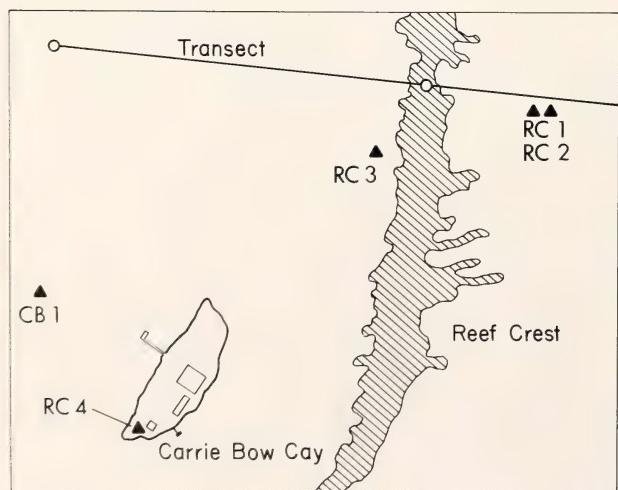


FIGURE 45.—Map of immediate Carrie Bow Cay area showing rotary core locations (RC1–RC4) and the easternmost sediment vibrocoring location (CB1).

and effects of storms on Belizean islands, including Carrie Bow Cay, have been described by Stoddart (1962, 1963).

Vibrocoring locations are shown in Figures 44 and 46 and rotary drill core locations are shown in Figures 45 and 46. Core RC2, immediately adjacent to RC1, was taken on a spur (Figure 47). This core was compared with core RC1, taken in a groove, to determine whether the spur and groove system was formed by erosion, as

proposed by Cloud (1959) for Saipan reefs or by construction, as proposed for Jamaica reefs by Goreau (1959) and determined for a Florida reef by Shinn (1963).

This work, conducted on and around Carrie Bow Cay, is part of a larger United States Geological Survey Belize project, the objectives of which are to determine (1) porosity distribution as controlled by submarine cementation, (2) factors that control reef distribution, (3) nature and origin of the numerous patch reefs lagoonward of the barrier reef, and (4) rate of sediment accumulation during the past 10,000 years. Only that work conducted on and around Carrie Bow Cay is reported here.

**ACKNOWLEDGMENTS.**—We gratefully acknowledge the gracious cooperation of the Belize government, in particular the fisheries department. This work would not have been possible without the aid of R. Gaenssen, owner and captain of the M/V *Sea Angel*. We also acknowledge the invaluable aid of P. Shea, who acted as diver and technician. The adapted jackhammer used in sediment vibrocoring was designed and perfected by D. Lanesky of the Comparative Sedimentology Laboratory, University of Miami, Fisher Island Station, Miami Beach, Florida. The use of brand names in this report is for descriptive purposes only and does not constitute endorsement by the United States Geological Survey.

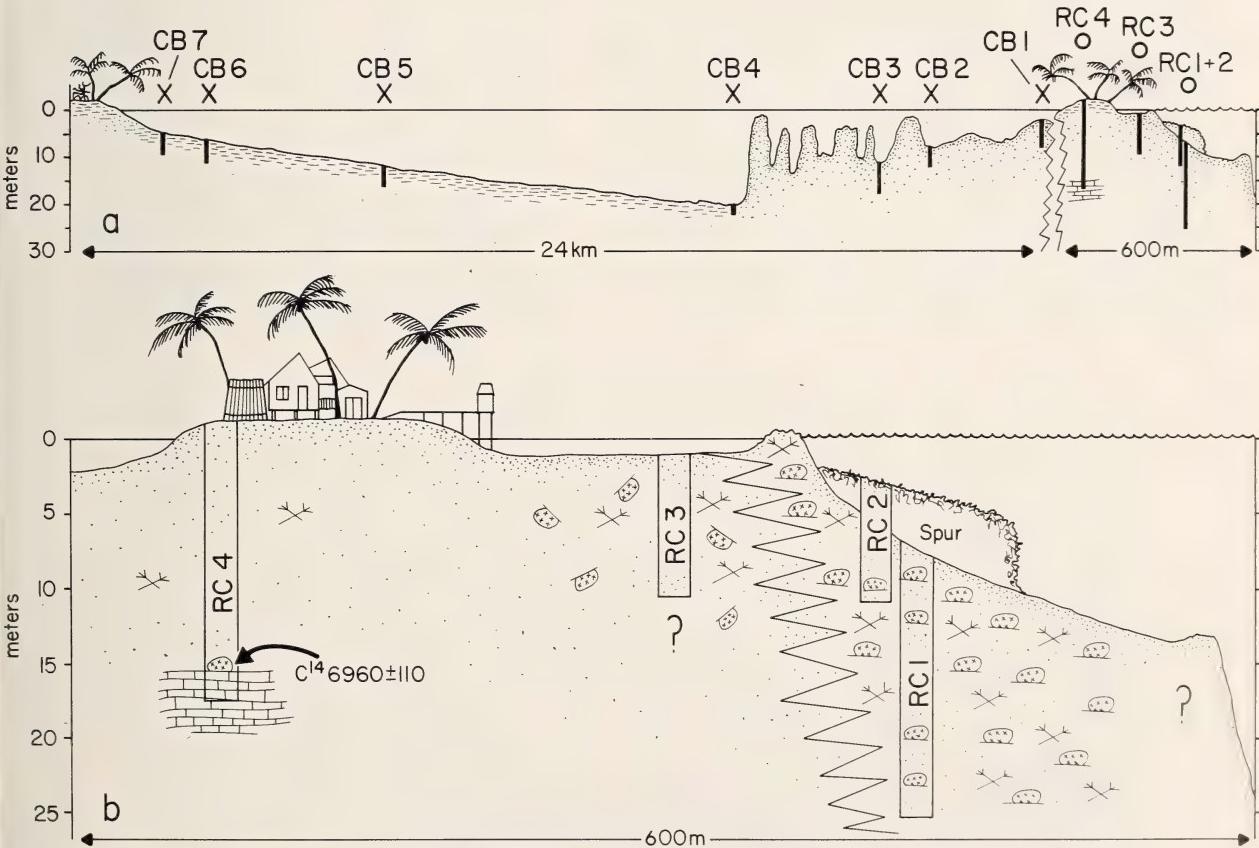


FIGURE 46.—Cross sections of study area: *a*, entire area shown in Figure 44, with vibrocore (CB) and rotary core (RC) locations; *b*, detailed cross section of Carrie Bow Cay and associated reef area comparable to Figure 45. Note distribution of corals seaward of reef crest, which is composed of coral rubble encrusted with *Millepora* sp. The inferred transition zone from in situ coral accumulation to sand and rubble is indicated by the zig-zag line. Staghorn corals shown near cores RC3 and RC4 are inferred. Staghorn corals in RC1 and RC2 were recovered because of cementation. RC1 and RC2 are at the same distance along the E-W section, RC2 being immediately to the N of RC1. (For explanation of symbols, see Figure 47.)

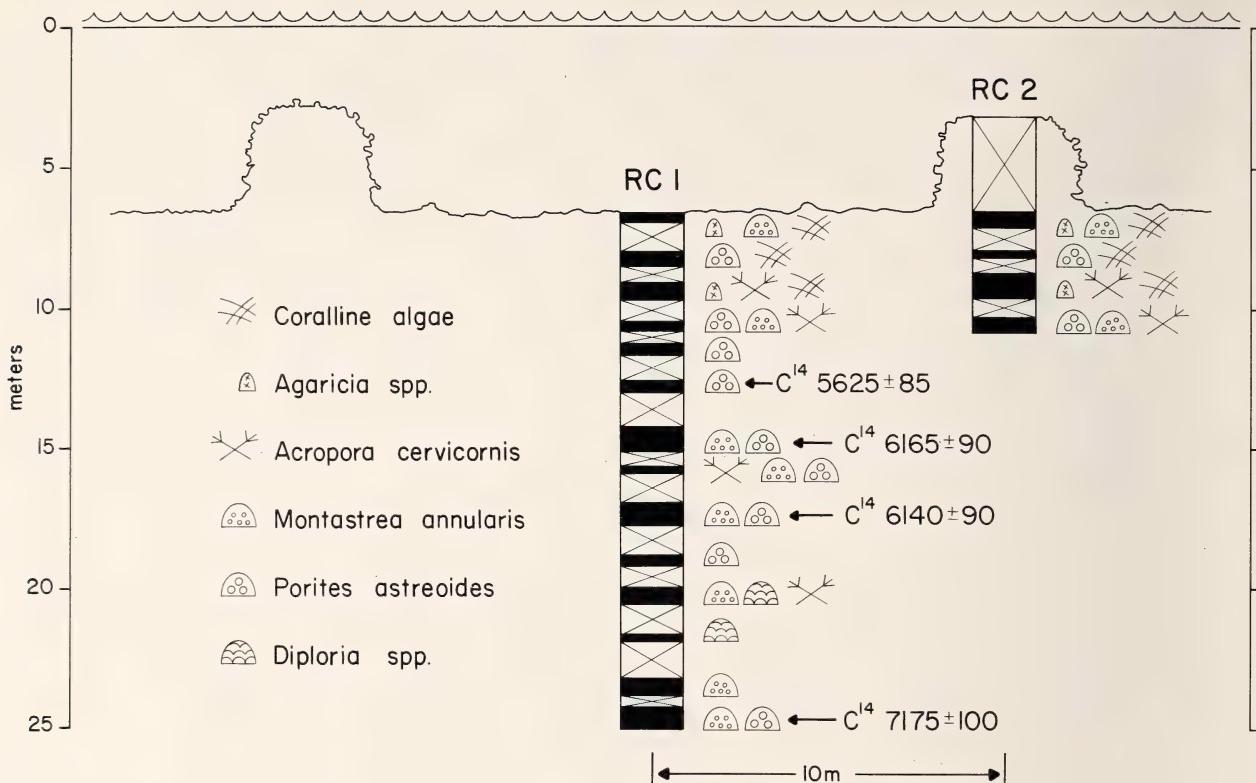


FIGURE 47.—N-S cross section between cores RC1 (drilled in a groove) and RC2 (drilled on adjacent spur) showing distribution of major coral components. Radiocarbon dates indicate that the section is less than 7175 years old and that growth rates are rapid. See Table 6 for accumulation rates. Also note apparent date reversal in corals between 14 and 17 m. Both ages are within the margin of error for the method; the samples should therefore be considered approximately the same age. These two dates indicate an extremely rapid rate of accumulation for that interval.

## Methods

**ROTARY DRILL CORING.**—Core drilling into the reef (Figure 48a) was accomplished with a version of the underwater hydraulic rotary drill described by Macintyre (1975). Modifications include (1) a portable, lightweight power source (manufactured by Custom Hydraulics of Miami, Fla.) measuring 1 m in length, 60 cm in width, 80 cm in height, and weighing only 125 kg, which is easily operable from a small skiff; (2) a lightweight plastic hydraulic hose,  $\frac{1}{2}$  inch (12.7 mm) in diameter; and (3) a lightweight, collapsible aluminum drilling tripod (Figure 48a). Standard length (5 ft, 1.5 m) N drilling rods and both X

and BX diamond-tipped core barrels were used.

Although the spur and groove zone was drilled to a depth of 18 m (RC1), only nine meters of the reef flat could be penetrated because of collapsing sand. Drilling the sands of Carrie Bow Cay required drilling mud, but commercial drilling mud

FIGURE 48.—Underwater coring equipment employed: a, diver-operated hydraulic drilling rig at location of RC1; b, hydraulic jackhammer in operation; c, equipment used for vibrocoring (A = hydraulic jackhammer; B = adapter that mates jackhammer to core tube; C = plastic cap for capping core before extraction; D = section of 3-inch (76 mm) diameter aluminum core tubing, with vents for letting out water as core is taken; E = aluminum clamps with handles used for extracting core from sediment).



was not available; a mixture of clay and silt dug from an area near Stann Creek on the mainland and diluted with sea water sufficed to accomplish the drilling. Five garbage cans containing sediment were brought to the island and dumped into a pit lined with plastic. The diluted mixture, necessary to prevent collapse of the hole, was used to drill the site near the south tip of Carrie Bow Cay to a depth of 16.2 m, where Pleistocene limestone appeared. Total depth including Pleistocene bedrock was 17.7 m.

**VIBROCORING.**—Sediment vibrocoring (Figure 48b) was accomplished by adapting a 36 kg hydraulic jackhammer (manufactured by Fairmont Hydraulics of Fairmont, Minn.), similar to the familiar air-powered jackhammers used to break up concrete, so that it could use 6 and 9 m lengths of standard 3 in (7.6 cm) aluminum irrigation tubing. The advantages of this hydraulic equipment were reduced corrosion and the ability to utilize the same hydraulic power source as that used for rotary drilling. The jackhammer was joined to the thin-walled tubing by an adapter that was constructed by press fitting an internally fitted steel sleeve to a standard, hardened steel chisel made especially for the hammer. The sleeve is a friction-fitting device that slips approximately 10 cm into the tubing. Further insertion is prevented by a collar (Figure 48c).

Water is able to escape from the core tubing as it penetrates sediment by means of relief ports added near the upper end of the tubing (Figure 48c). Slits were cut into the tube with a hacksaw and one side of each cut hammered inward, so that the resulting ports resemble gill slits. Initially, ports were made with an electric drill, but the saw and hammer method was found to be more efficient.

Coring was accomplished by attaching either the 6 or 9 m lengths of tube to the jackhammer and floating the entire device with an inverted air-filled garbage can. When the core tube was vertical over the selected site, one diver released air from the garbage can while another diver guided the unit to the bottom. When the tube contacted bottom, the diver depressed the trigger

and the machine-gun action of the hammer drove the core tube into the sediment (Figure 48b). Generally, 6 to 9 m of penetration was achieved in less than 30 seconds with an average of 80 percent recovery. In very clear water the tube was first driven approximately  $\frac{1}{2}$  m vertically into the bottom with a 1 kg sledge hammer. When the tube was correctly oriented and free standing, the jackhammer was floated into position and attached to the adapter, and coring began. Because the tube itself does not rotate during coring, orientation of the core can be determined by putting a scratch on one side of the soft aluminum tube before extracting the core from the bottom.

Cores were removed from the bottom with the aid of adjustable clamps with handles that were attached to the tube at the sediment/water interface. Excess tubing was sawed off underwater by hacksaw. An externally fitting plastic cap (Caplug EC-48, manufactured by Capplugs Division of Protective Closures Company, Inc., Buffalo, N.Y.) was affixed to the protruding tube end, thereby creating a vacuum and preventing loss of core material from the buried end during extraction. The cores were extracted and brought to the surface by attaching the garbage can and filling it with air from the SCUBA regulator. Although core catchers were not used, sediment was seldom lost during extraction.

All vibrocores were dried and impregnated with plastic according to the methods of Ginsburg et al. (1966). Peats were removed prior to impregnation. Carbon-14 dating was carried out at the University of Miami's Radiocarbon Dating Laboratory.

Sediment types are described according to the classification of Dunham (1962). In keeping with his scheme, loose sediment is described as if it were the rock it will eventually become. Thus, "packstone" is used to describe sand-size carbonate grains whose interstices are filled with lime mud; "grainstone" is used if mud is absent. In addition, mud-supported sediments are termed "mudstones" if they contain less than 10 percent sand-size grains and "wackestones" if they have more than 10 percent.

## Results

**OUTER REEF.**—Of the four cores drilled in the Carrie Bow Cay area, only RC1 and RC2 contained in situ corals. Core RC1 from a groove in 7 m of water was by far the most difficult to drill (see Figures 45, 46, 47). The core was drilled to 18.3 m before caving and other difficulties prevented further penetration. Pleistocene bedrock was not encountered. Table 5 shows that core recovery was about 36 percent. Core RC2, approximately 10 m to the north on the adjacent spur, was drilled to a depth of 7.6 m, the first 3.7 m being in the spur. Because the spur is composed primarily of the lettuce coral, *Agaricia* sp., and little cementation or infill of internal sediment is present, there was practically no core recovery in this interval. Recovery of material began when the drill reached the level of the adjacent groove. Because the material from both groove and spur base was identical, we concluded that the spur is of constructional origin. We recognize, however, the possibility of a deep-seated erosional spur and groove in the Pleistocene strata below 18 m which might serve as a template for later growth. Nonetheless, the visible portion of the spurs in this area is clearly constructional, and the interval 3.7 to 7.6 m (below the spurs) is probably also constructional.

The most noticeable feature in core RC1 and the lower 3.7 to 7.6 m of RC2 is the occurrence of both cemented and uncemented internal sediment. Fine-grained internal sediment was generally light gray in color and contained sedimentary laminations, commonly inclined. The cement is Mg-calcite, similar to that reported elsewhere (Ginsburg et al., 1967; Macintyre et al., 1968; James et al., 1976; Land and Goreau, 1970; Macintyre, 1977; Shinn, 1969, 1971). In partially filled small cavities (less than 1 cm across), internal sediment is commonly geopetal, that is, the upper surface of the fill is horizontal. In larger voids, however, such fillings are generally inclined (Figure 49). Very little uncemented sediment was recovered from large voids, but its presence was indicated by bursts of muddy drilling water as-



FIGURE 49.—Two pieces of core from RC1: *a*, section from 10.75 m showing cemented internal sediment at steep angle (arrow); note unusual network of voids in cemented internal sediment; cause of the void network is not known, although it does not appear to be caused by leaching; *b*, sample from 7.4 m; gray internal sediment resting on *Porites* coral; note steeply inclined laminations within cemented internal sediment. Cement is Mg-calcite; origin of voids is not known, but they are thought to be organic borings.

sociated with sudden drops of the drill bit and by small amounts of sediment recovered in the cores.

Fibrous aragonite, probably the most diagnostic form of submarine cement, was present only in small cavities, usually within shell and coral chambers, and was visible only in thin sections. This observation is identical to that reported by Macintyre (1977) but is in strong contrast to the fibrous aragonite crystals 1 to 2 cm long described by Ginsburg and James (1976) and James and Ginsburg (1978) from the deep fore reef at Belize below 100 m.

**REEF FLAT AND ISLAND.**—Core RC3 was drilled on the reef flat approximately 15 m behind the reef crest in water about 25 cm deep. The seabottom at the RC3 site consisted of a hard pavement

composed of cemented sediment sparsely populated by small head corals. Drilling showed the pavement to be only 1 cm thick and underlain by coral rubble imbedded in coarse carbonate reef sand. From approximately 2 m to total depth (8.8 m), only carbonate sand with sparsely scattered coral fragments was encountered. Except for the thin cemented pavement exposed at the surface, no evidence of submarine cementation was found, nor did any corals appear to be in growth position.

Core RC4 was drilled on the southwest tip of

Carrie Bow Cay (Figures 45). Drilling revealed a section consisting mainly of coarse-grained carbonate sand. At a depth of 15.5 m, a single large head of *Siderastrea siderea* appeared in growth position on Pleistocene bedrock. Bedrock was reached at 16.2 m and cored to 17.7 m. It is coralline limestone that has been leached and contains brown caliche staining. The coral overlying the bedrock was dated by carbon-14 technique and is discussed below. There was no evidence of cementation of the Holocene sands beneath Carrie Bow Cay.

TABLE 5.—Locations, water depths, core recovery, and general comments on rotary drill cores and sediment vibrocores taken in the Carrie Bow Cay area, Belize

Core	Location		Water depth (m)	Core hole depth (m)	Recovery (m)	Comments
	Lat., Long.	Description				
<b>ROTARY DRILL CORES</b>						
RC1	16°48'13"N, 88°04'41"W	About 60 m seaward of reef crest	6.7	18.3	6.55	Drilled in groove
RC2	16°48'13"N, 88°04'41"W	10 m N of core RC1	3.7	7.6	1.8	Drilled on spur; recov- ery only below base of spur
RC3	16°48'13"N, 88°04'43"W	On reef flat 15 m W of reef crest	0.25	8.8	≈0.5	Poor recovery due to uncemented sand
RC4	16°48'10"N, 88°04'45"W	SW tip of Carrie Bow Cay	+0.5	17.7	≈0.03	No core recovery above 15 m; good recovery from Pleistocene 16.2–17.7 m
<b>VIBROCORES</b>						
CB1	16°48'10"N, 88°05'10"W	About 150 m W of Carrie Bow Cay	2.5	4.6	3.7	Carbonate sand bot- tom with scattered <i>Thalassia</i> species
CB2	16°47'50"N, 88°06'30"W	S of Twin Cays	7.3	3.5	2.8	Peat extends from about 2.3 m to bot- tom of core recovery at 2.8 m
CB3	16°49'30"N, 88°07'45"W	See Figures 44 and 45	11.5	5.4	5.0	Contains peat from 4.5 m to bottom of core recovery at 5.0 m
CB4	16°50'20"N, 88°08'40"W	Just W of dropoff into Victoria Channel	20.2	2.0	1.6	Sticky red clay pre- vented further core penetration
CB5	16°53'25"N, 88°14'00"W	See Figures 44 and 45	12.2	3.4	2.7	Peat in bottom 50 cm of core; water visibility about 25 cm
CB6	16°54'15"N, 88°15'50"W	~2 km from mainland	6.7	3.9	3.7	Peat in upper section of core; see Table 6
CB7	16°54'15"N, 88°15'88"W	~300 m from shore	4.3	3.1	2.4	Bottom 3/5 of core is peat

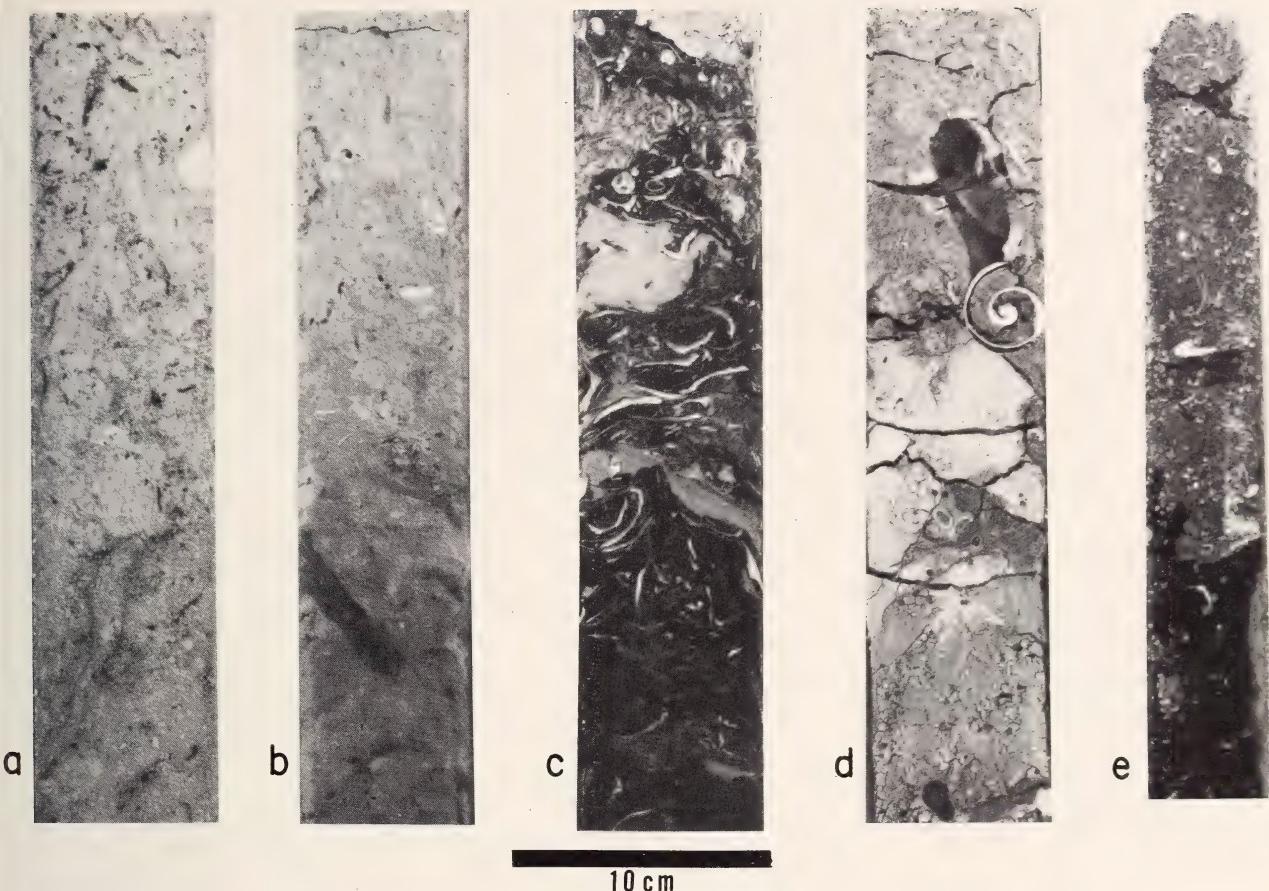


FIGURE 50.—Selection of plastic-impregnated sediment cores from transect shown in Figure 44: *a*, core CB1, interval 40 to 70 cm; note burrowing, grass roots, and coral fragment at upper right; smaller white fragments are *Halimeda*; *b*, same interval from core CB2; note large burrow; *c*, core CB2 from interval 2.2 to 2.5 m showing transition from lime sediment to peat; note coral fragments at top, *Oculina* sp., and large unidentified oysters and other mollusks at transition; *d*, core CB4 showing transition from carbonate grainstone to orange terrigenous clay, contact is at base of large gastropod, cracks in lower part of core are due to dessication in clay, which would not impregnate because of its fine-grain size; *e*, top of core CB6 (interval 0 to 30 cm); upper portion consists of coarse, poorly sorted quartz sandstone merging with peat near bottom; large white fragments are quartz pebbles.

VIBROCORE TRANSECT.—Location of all seven vibrocores is shown in Figures 44 and 46, and brief comments on depth, location, and penetration appear in Table 5. Selected photographs of these plastic-impregnated cores are shown in Figure 50.

Core CB1 consists entirely of burrowed, reef-derived grainstone but lime silt content increases slightly near the base, locally creating a packstone facies associated with burrows. Despite a few

sticks of *Acropora cervicornis*, the principal sand-size constituents are *Halimeda* plates and soritid foraminifera. *Homotrema* sp., a foraminifer generally abundant in reef-derived sands, is rare.

Core CB2 is predominantly a packstone mottled by abundant burrows. Mollusks are the most obvious large fossils and soritid foraminifera are abundant, approximately as abundant as *Halimeda* plates. At 2 m, there is a transitional change to lime silt, grading into a mixture of peat and

lime silt. Large oyster shells are mixed into the peat down to 2.7 m. Broken oyster shells extend deeper. Coral fragments of *Oculina* sp. occur between 2.1 and 2.2 m, just above the peat.

Core CB3 consists of burrowed packstone and silty lime mudstone with pelecypods to 3.7 m. Sediment becomes darker at 3.7 m owing to abundance of peat flecks. Pelecypods occur between 4 and 5 m. Sediment is lime silt between 4 and 4.5 m with an admixture of clay that gives it a gray-brown color. Peat begins at 4.5 m and extends to the bottom of the core at 5 m. Gastropods, such as *Astrea* sp. and various cerithids, occur just at the transition from lime sediment to peat.

Core CB4 was taken in 20 m of water immediately landward of a continuous shallow rock ridge (see Figure 46). The upper 1 m of the core consists of burrowed mixed grainstone and packstone. The grains are *Halimeda*, mollusk fragments, and foraminifera. Soritid foraminifera are rare, and obvious darkened grains make up 1 to 3 percent of the section. At 1.24 m the lime sediment changes into brownish-orange clay containing red-brown concretions. The unexpected occurrence of such coarse-grained sediment at this depth is probably explained by the nearby shallow ridge. Sediment is probably periodically swept landward off this ridge.

Core CB5 consists of brown mud and wackestone with terrigenous clay containing scattered mica flakes. The predominant fauna is small, thin-shelled pelecypods. At 2.3 m there are large oyster shells, and at 2.5 m the sediment grades to a darker color clay and organic-rich mudstone. Peat was collected from 1.78 and 2.67 m for dating.

Core CB6 consists of 30 cm of very poorly sorted quartz sandstone with quartzite pebbles up to 1 cm in diameter. The only carbonate is pelecypod fragments. Peat begins at 30 cm and extends to 1.3 m. The remainder of the core down to 3.65 m consists of massive, dirty sandstone with root marks. Between 3.65 m and the bottom of the core at 3.7 m, the sediment is gray clay with bright-red clay mottles.

Core CB7 consists of almost 1 m of burrowed,

poorly sorted quartz sandstone with pelecypod fragments, scattered *Halimeda* plates, and few gastropods. Sediment contains peat fragments and abundant quartzite pebbles at 75 cm. The section becomes peat at 0.92 m, and peat extends to the bottom of the core at 2.4 m. The peat contains thin stringers of quartzite pebbles.

Peat was exposed on the bottom in 1 m of water landward of site CB7, and a peat-forming swamp is present at sea level all along the shore, just landward of a thin quartz-sand beach ridge. The change from coarse-grained carbonates to terrigenous clastics and peats in a shoreward direction follows the basic pattern described by Purdy et al. (1975).

Although red mangroves are abundant on the seaward edge of the swamp, numerous hardwoods, grasses, and small palms indicate the peat is not entirely of mangrove origin. Nevertheless, the peat is accumulating at sea level and can be visually correlated with the submarine peat just offshore and is thought to be continuous with the peat in cores CB6 and CB7.

RADIOCARBON AGE DATING—Corals from various depths within the rotary cores RC1 and RC4 were sampled and dated by the radiocarbon method, as were peats from sediment vibrocores CB5, CB6, and CB7. Dates, calculated accumulation rates, and sediment and water depths are provided in Table 6. In this table there are two columns of figures under the heading “Accumulation rates (m/1000 y)”. The first column (core top to sample) lists the accumulation rates in meters/1000 years, assuming the top of the reef is growing and has a <sup>14</sup>C age of approximately zero. The second column (intervals between samples) lists the calculated accumulation rates between dated samples. This figure is more meaningful for obvious reasons. All peat dates were obtained by D. S. Introne in 1978 at the University of Miami’s Radiocarbon Dating Laboratory. Coral material was dated at the same laboratory by J. J. Stipp.

It can be seen from Table 6 that the reef off Carrie Bow Cay has been growing upward at a rapid rate (ranging from approximately 1 to 6 m/1000 y), considerably faster than accumulation of the lagoonal sediments overlying the peats

TABLE 6.—Radiocarbon dates and accumulation rates (m/1000 y) of selected material in rotary drill cores and sediment vibrocores (further explanation in text; location coordinates listed after each core number; note unexplained age reversal in two samples from RC1)

Core		Lab. no.	Material dated	Depth in core hole (m)	Interval between samples (m)	Water depth (m)	Depth from water surface to sample (m)	Age difference between samples (y)	Accumulation (m/1000 y)	
									Core top to sample	Intervals between samples
RC1	16°48'13"N, 88°04'41"W	UM-1009	<i>Montastrea annularis</i>	5.79	2.44	6.7	12.49	540	5625±85	1.03
		UM-1010	<i>Porites</i> sp.	8.23	2.74	6.7	14.93	0	6165±90	1.33
		UM-1011	<i>M. annularis</i>	10.97	6.70	6.7	17.67	1035	6140±90	1.79
		UM-1012	<i>Porites</i> sp.	17.67		6.7	24.37		7175±100	2.46
RC4	16°48'10"N, 88°04'45"W	UM-1013	<i>Siderastrea siderea</i>	15.54		+0.5	15.04		6960±110	2.23
		UM-1249	Peat	1.78	0.89	12.2	13.98	618	7619–320	0.23
CB5	16°53'25"N, 88°14'00"W	UM-1250	Peat	2.67		12.2	14.87		8237±270	0.32
		UM-1252	Peat	0.30		6.7	7.00		6804±150	0.04
CB6	16°54'15"N, 88°15'50"W	UM-1251	Peat	0.62	0.32	6.7	7.32	2004		0.16
		UM-1248	Peat	0.92		4.3	5.22		8808±600	0.07
CB7	16°54'15"N, 88°15'88"W								2861±190	0.32

(<1 to  $\approx$  1.4 m/1000 y). This agrees with Purdy's (1974a) observation of an approximately 10 to 1 difference in accumulation rate between the barrier platform and the shelf lagoon. Our reef accumulation rates exceed rates determined for the Florida reef tract. Shinn et al. (1977) determined accumulation rates in Florida to range from 0.38 m/1000 y to 4.85 m/1000 y. More rapid accumulation rates have been reported at Alacrán Reef (north of the Yucatán Peninsula in the Gulf of Mexico) by Macintyre et al. (1977), where the average of four dated intervals is 5.6 m/1000 y and one interval indicates a rate of 12 m/1000 y. Further discussion of reef accumulation rates, both in the Atlantic and Pacific, has been provided by Adey (1978).

## Discussion

Figure 46 is an interpretation of facies changes across the Carrie Bow reef. Core RC3 on the reef

flat just behind the reef crest clearly demonstrates that the reef flat is not composed of corals that have grown up to sea level, but instead is composed of reef sands and some rubble, which have probably been thrown up and over the reef crest during storms. In many areas along the lagoonward edge of the reef-flat sands, patch reefs are in the process of being buried as these sands accrete landward to extend the reef flat. Reefs off the Florida Keys are also growing landward (Shinn et al., 1977). From his work on Alacrán Reef, Logan (1969:189) termed such accumulations off-reef clastic drape reefs (model 3).

If underlying topography accounts for the location of Carrie Bow Cay, the proof cannot be found in our drilling. Previous work (Halley et al., 1977) proved conclusively, however, that Boo Bee Patch Reef, near Wee Wee Key about 8 km to the southwest, was initiated over a 6 m Pleistocene topographic high. Drilling on two mangrove islands situated on patch reefs also con-

firmed Pleistocene bedrock topography to be the controlling factor. In both cases Pleistocene coralline limestone reached to within 12 m of sea level under the island. Surrounding the island, the rock was more than 21 m below sea level. On the basis of his 1960 studies, Purdy (1974a,b) was the first to suggest that rock floor topography is the factor controlling island distribution on the Belize shelf. We suspect, therefore, that the reef off Carrie Bow Cay was initiated on a pre-existing rock high and that initial flooding, determined by <sup>14</sup>C age of coral growing directly on bedrock (see Table 6), occurred before approximately 7000 y BP. Whether there has always been an island since early Holocene flooding or whether the island (actually little more than a sand spit) sprang into existence during the past few thousand years has not been determined.

On the basis of our observations and drilling, the spurs and grooves appear to be relatively recent in age and clearly are not of erosional origin. Because the Holocene reef is greater than 18 m thick, however, it seems unlikely that the present day spur and groove systems have existed in the same place throughout the reef's history. This conclusion cannot be borne out by only two core holes. We suspect that such a system has existed in the past but that the position of the spurs and grooves has shifted laterally as the reef built up. Furthermore, it seems unlikely to us that the present system is simply patterned over a Pleistocene spur and groove system more than 18 m below the present reef surface.

Determining the origin of the spur and groove system at Carrie Bow Cay reef was beyond the purpose of the expedition; however, such a determination should be made. We encourage coral reef researchers to drill spur and groove systems at many sites in the Caribbean or Pacific to determine the significant factors that lead to spur and groove development.

### Conclusions

The Holocene coral reef seaward of the reef crest is in excess of 18 m thick. The present spur and groove system is constructional. The reef flat is composed primarily of reef-derived carbonate sand with scattered coral rubble. Carrie Bow Cay is Holocene and composed primarily of carbonate sand over 15 m thick. Leached calcitic limestone, which was subaerially exposed during the last glacial period, underlies the island at a depth of 16 m. Flooding of the bedrock occurred prior to 7000 years ago. Submarine cementation is, for the most part, restricted to the Holocene section seaward of the reef crest. Except for a thin exposed pavement directly shoreward of the reef crest, all reef flat and lagoonal sediments over a distance of 24 km are uncemented. Peat, representing former sea level, occurs in sediment cores in the lagoon. Peat in cores near the mainland overlie terrigenous clastic sediments; thus, the peats probably record the initial flooding of the coastal plain during the most recent transgression.

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# Terrestrial Environment and Climate, Carrie Bow Cay, Belize

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## ABSTRACT

Severe hurricane activity during the past 20 years has reduced Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ) to half its pre-1960 size of 0.8 ha. At present, Carrie Bow Cay (0.4 ha area) is one of the smallest inhabited sand cays on the barrier reef of Belize. The island measures  $120 \times 36$  m, rises 40 cm above mean tide level, and supports three wooden cottages with freshwater tanks. The only permanent terrestrial plants are about 60 coconut trees. Other vegetation appears periodically and spreads until it is destroyed by intermittent storm tides. Conspicuous animals include a few birds, a lizard, and some supratidal crustaceans. About one-third of the island's surface is intertidal and occupied mainly by algae, crustaceans, and mollusks that are adapted to this habitat. The climate is oceanic and is dominated largely by northeasterly trade winds.

## Introduction

Previous terrestrial investigation of Carrie Bow Cay was based on brief topographic and floristic surveys (Stoddart, 1963; 1969; 1974) and a short-term meteorological study (Kjerfve, 1978). Our own first topographic survey was prompted by the severe impact of hurricane Fifi, in 197, on the shape and size of the island. From then on we monitored morphological changes of the cay, con-

dition of the remaining coconut tree population, and recovery of the vegetation that had been entirely eliminated by salt water flooding. Our other observations on the terrestrial and intertidal flora and fauna of the islet are of casual qualitative nature and restricted to large and conspicuous organisms. Meteorological records were taken regularly during the months of our field work, mainly in spring and early summer, but are sporadic during the remaining parts of the year. Carrie Bow Cay has been the base of the Smithsonian Institution coral reef study since the initiation of the program in 1972. The small island provided the necessary support in close proximity of reef and lagoon habitats without having noticeable terrestrial effects on these environments.

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## Methods

**GEODETIC SURVEYS.**—Tape measure, sighting compass, and sighting along permanent or temporary markers were used for determining shape and size of the island and position of trees and artificial structures. The concrete boat dock on the lagoon side and the wooden main house in the center of the cay provided the principal points of reference. Vertical photographs from a helicopter, in March 1976, helped to improve the documentation of the island's physiography.

**PLANT ABUNDANCE.**—The first quantitative survey of plants made in 1978 consisted of subjective visual estimates of five categories of relative abundance. More objective measurements of area of plant coverage were made in 1979 by placing a  $50 \times 50$  cm ( $0.25 \text{ m}^2$ ) frame subdivided into  $10 \times 10$  cm ( $100 \text{ cm}^2$ ) fields over all surfaces of the island showing vegetation. The number of frames occupied by a given species was recorded to the nearest half frame ( $50 \text{ cm}^2$ ).

**METEOROLOGY.**—Generally, meteorological conditions were recorded three times a day (0600–0800 h; 1200–1400 h; 1800–2000 h) whenever the laboratory on Carrie Bow Cay was in operation, most commonly during the periods January–June and October/November, 1976–1978. Temperature was measured with  $\pm 0.5^\circ \text{ C}$  accuracy in shaded air, in sun-exposed sand (5 cm below surface), in water on the reef flat (0.2 m average bottom depth), and below low-tide level at the boat dock (lagoon, 0.8 m average bottom depth). Some continuous analog chart recordings of solar radiation were made by pyranograph (WeatherMeasure B211). Wind speed and direction were read from a cup anemometer with air foil vane (WeatherMeasure W121). Precipitation was measured with two rain gauges (10 cm diameter), one

installed on the cay, and the other one on the mainland at Pelican Beach Motel, Dangriga. The rainy season (June–September) of 1979 was also monitored by an unattended tipping-bucket雨量器 (WeatherMeasure P501-I) with solar-powered event recorder on Carrie Bow Cay. Humidity was calculated from psychrometer (Psychro-Dyne PP100) readings.

## Physiography

**LOCATION.**—Carrie Bow Cay ( $16^\circ 48' \text{N}$ ,  $88^\circ 05' \text{W}$ ) is a small sand island located on top of the barrier reef that lines the outer shelf edge of Belize (formerly British Honduras), Central America (Plate 1: *center right*). Its former name, Ellen Cay, is still recorded on many nautical charts. The nearest significant settlement is Dangriga (Stann Creek), a town of 7000 inhabitants on the mainland, 24 km due  $320^\circ$  (NW). The cay belongs to H.T.A. Bowman of Dangriga and is used as a vacation place for his family. The nearest islands are South Water Cay, 1.5 km due  $0^\circ$  (N), a sand cay populated by a few fishermen and occasional vacationers, and Twin Cays (also known as South Water Range) 4 km due  $323^\circ$  (NW), an uninhabited mangrove development. Carrie Bow Cay is protected from open ocean waves by a crescent-shaped reef crest to the east and a 100 m wide reef flat that extends from the crest to the island's seaward shore (Plate 5: *top left*).

**SHAPE AND SIZE.**—With a surface area of less than 0.4 ha, Carrie Bow Cay belongs among the smallest inhabited cays on the Belizean shelf (Stoddart and Fosberg, herein: 527) (Figure 51; Plate 1: *bottom left*). The island formerly was double its present size (H.T.A. Bowman, pers. comm.) and bordered by mangrove, but clearing of these trees in 1944 led to progressive erosion by storm tides. Stranded beachrock as far as 30 m east and south of the present seaward shore documents both a shift in dimensions and slow migration leewards. At present, the cay has an elliptical shape with approximate north-south exten-



FIGURE 51.—Carrie Bow Cay, aerial view from the south, May 1973; note exposed beach rock on the reef flat east of the island.

sion. The longer axis is directed due  $30^\circ$  (NNE) and measures 120 m between mean tide level (MTL) points; the greatest dimension perpendicular to this axis lies along a line transecting the center of the isle and measures 36 m. Surface area calculated from planimetry is 0.36 ha to MTL, 0.25 ha if only dry-land (supratidal) area is measured. Highest elevation, which is approximately 40 cm above MTL, occurs at the central portion of the island.

**SUBSTRATES.**—Reef-derived carbonate sand and rubble on a base of Pleistocene bedrock (Shinn et al., herein: 63) make up the entire natural substrate of the cay (Figure 52a). Accumulation of beach sand varies with the direction and force of wind and currents. Under the influence of the predominant northeasterly trade winds, sand is deposited at the north point and northwest beach and around the south tip; at

times separate intertidal sand spits are formed to the north. Concrete block seawalls and rubble and coral rock landfills built up over many years to delay erosion dominate the northwest (Figure 52b) and southeast shorelines, which also have a few small sandy beaches here and there. Conch shells abandoned by generations of local fishermen are accumulated along the southwest coast.

**STRUCTURES.**—Other than seawalls, artificial structures on Carrie Bow Cay include two docks and three buildings with water vats (Figure 51; Plates 1: bottom right, 5: top left). The main or boat dock to the west (lagoon side) of the cay is 26 m long and built of concrete. A smaller wooden dock over the reef flat (SE) serves the two out-houses. The buildings are wooden and include the main house,  $14 \times 12.5$  m, "Junior's House,"  $13 \times 3.5$  m (now serving as our project's laboratory), and a small cabin,  $5 \times 5$  m (Figure 60).



FIGURE 52.—Intertidal substrates: *a*, sandand rubble (mainly conch shells) on western shore, looking north (coconut palms felled by hurricane Greta); *b*, northwest seawall, coated by algae *Cladophoropsis* and *Oscillatoria*, toppled by Greta.

### Flora and Fauna

Carrie Bow Cay's small size, lack of a freshwater lens, and exposed location near the open ocean are responsible for the absence of a complex permanent terrestrial environment. We distinguish between an intertidal zone along the shore and a central island area above the high-tide

beach undercut, which, in our experience, has been flooded by sea water only during hurricane tides (see below).

**SUPRATIDAL ORGANISMS.**—The most conspicuous, and only permanent, plants, except perhaps for the lichens, are coconut palms (*Cocos nucifera* L.) most of which were planted during the past 35 years in at least five recognizable N-S rows. In

May 1979 this population consisted of 58 healthy trees, of which 38 were mature and showed either nuts or flowers, 8 were immature (one or more years established), and 12 were freshly planted after hurricane Greta (less than one year estab-

lished). The remaining vegetation observed in May 1978 and May 1979 (before and after hurricane Greta; Table 7) recolonized Carrie Bow Cay after salt water flooding associated with hurricane Fifi (September 1974) had washed away

TABLE 7.—Systematic list and relative abundance of Carrie Bow Cay plants, excluding coconut and others artificially introduced; figures for 1978 show recolonization of the island after hurricane Fifi (September 1974), when all vegetation was destroyed, and are visual estimates; data for 1979 reflect minor changes and losses (indicated by dash) in plant cover caused by hurricane Greta (September 1978) and are compiled from quadrat counts (see "Methods"); likely methods of dispersal are indicated for each plant (B = bird, D = drift, W = wind); approximation of size and frequency of plants is given for 1978

Species (Family)	1979				Method of dispersal
	1978 $m^2$	$m^2$	% total	rank	
<i>Paspalum distichum</i> L. (Gramineae)	>5	0.010	0.08	9a	D?
<i>Sesuvium portulacastrum</i> (L.) L. (Aizoaceae)	0.02–0.50*	2.585	19.94	3	D?, B?
<i>Philoxerus vermicularis</i> (L.) Beauvois (Amaranthaceae)	0.02–0.50*	—	—	—	D, B?
<i>Suaeda linearis</i> (Elliott) Moquin (Chenopodiaceae)	<0.01	0.015	0.12	8a	D, B?
<i>Portulaca oleracea</i> L. (Portulacaceae)	1–5**	4.825	37.22	1	B?
<i>Coccoloba uvifera</i> L. (Polygonaceae)	<0.01	—	—	—	D, B?
<i>Cakile lanceolata</i> (Willdenow) O. E. Schulz (Cruciferae)	0.5–1.0†	3.275	25.26	2	D
<i>Rhizophora mangle</i> L. (Rhizophoraceae)	—	0.010	0.08	9b	D
<i>Euphorbia blodgettii</i> Engelmann ex Hitchcock (Euphorbiaceae)	1–5**	0.185	1.43	6	B?
<i>Euphorbia mesembrianthemifolia</i> Jacquin (Euphorbiaceae)	1–5**	1.820	14.04	4	B?
<i>Ipomoea pescaprae brasiliensis</i> (L.) van Ooststroom (Convolvulaceae)	>5	0.190	1.47	5	D
<i>Ipomoea stolonifera</i> (Cyrillo) Gmelin (Convolvulaceae)	<0.01	—	—	—	?
<i>Tournefortia gnaphalodes</i> (L.) Kunth (Boraginaceae)	<0.01	0.035	0.27	7	D
<i>Eclipta alba</i> (L.) Hasskark (Compositae)	<0.01	—	—	—	W, B?
Unidentified seedling					
1	<0.01	0.015	0.12	8b	D
2	<0.01	—	—	—	D
Total plant cover	not determined	12.965	100.03		

\* few medium-sized plants, each 0.02–0.30  $m^2$

\*\* numerous small plants, each 0.01–0.02  $m^2$

† few large plants, each >0.3  $m^2$

or killed all plants except the majority of coconut trees (Figure 53). In addition to the species listed in Table 7, two were recently artificially introduced: *Casuarina equisetifolia* L. (Casuarinaceae) and *Hymenocallis littoralis* (Jacquin) Salisbury (Liliaceae, sensu lato). At least three species of lichens are common on the northeast surfaces of wind exposed palm trunks: *Lecanora subfusca* (L.) Acharius, *Pyxine cocoes* (Swartz) Nylander, and *Chiodescon* sp.

Although we have noted a variety of insects and a few spiders on Carrie Bow Cay, we have not determined the species and do not know whether they are breeding resident populations. Some ants, cockroaches, and spiders are no doubt

introduced by supply boats carrying produce. Fleas and ticks have been left behind by dogs, the former at times plaguing sensitive investigators. Flying insects are commonly blown over from land or larger islands during westerly winds. Most of the island's invertebrate fauna, however, consists of three crustaceans: the hermit crab *Coenobita clypeatus* (Herbst), and the crabs *Ocypode quadrata* (Fabricius) and *Gecarcinus lateralis* (Freminville).

Only the lizard *Anolis sagrei* Duméril and Bibron, a species widespread in the West Indies and apparently expanding its range onto Caribbean Mexico and Middle America (R. Crombie, pers. comm.), occurs as resident population of vertebrates on Carrie Bow Cay. A sea turtle, *Caretta caretta* (L.), was last seen laying eggs on the island on 28 May 1972 (A. Antonius, pers. comm.). Birds that feed regularly around the cay are the Brown Pelican (*Pelecanus occidentalis* L.), Frigatebird (*Fregata magnificens* Mathews), and Osprey (*Pandion haliaetus* (L.)). Other birds commonly seen include the Boat-tailed Grackle (*Cassidix mexicanus* (Gmelin)), Common Tern (*Sterna hirundo* L.), Brown Booby (*Sula leucogaster* (Boddaert)), Snowy Egret (*Leucophoyx thula* (Molina)), and Barn Swallow (*Hirundo rustica* L.). An assortment of involuntary visitors from the mainland, such as warblers and flycatchers, arrive exhausted on the island after periods of strong westerly winds. All birds, except the grackle and the swallow, roost elsewhere, most likely on South Water Cay. The grackle may even breed on Carrie Bow Cay because a female was observed gathering materials for nest building.

**INTERTIDAL ORGANISMS.**—The mean tidal range at Carrie Bow Cay is only 15 cm (Kjerfve et al., herein: 47, Table 4). The observed maximum range, however, partly because of wind forcing is more than 40 cm. With a shoreline slope of 90° to 4° the width of the intertidal zone on Carrie Bow Cay ranges between 40 cm on vertical cinder block walls and 6 m at the flat northern point, on the average between 0.5 and 2.0 m. Only during spring tides are wide areas on the reef flat exposed (Plate 1: bottom right).

Sandy beaches have a diverse and rich intertidal meiofauna (Kirsteuer, in prep.) but only one



FIGURE 53.—Plant cover on north point, May 1978: *Ipomoea pescaprae*, *Cakile lanceolata* (foreground, with 0.25 m<sup>2</sup> frame), and freshly planted *Casuarina* tree.

benthic macro-organism, the cerianthid *Arachnanthus nocturnus* den Hartog, could be observed at low tide buried in exposed sand on the northeast shore. *Ocypode quadrata* crabs, however, temporarily establish burrows in sand areas exposed at low tide.

Rocky substrates support a more varied intertidal flora and fauna but differences in abundance can be observed between the leeward (west) and windward (east) sides of the island. Coral rock, rubble, and concrete blocks of the leeward sea wall are thickly covered by algae (Figures 52b, 54a). *Oscillatoria submembranacea* Ardissonne and Strafforella and *Schizothrix mexicana* Gormont (Cyanophyta), and *Cladophoropsis membranacea* (C. Agardh) Børgesen (Chlorophyta) occupy the upper zone, *Padina jamaicensis* (Collins) Papenfuss (Phaeophyta) and *Neomeris annulata* Dickie (Chlo-

rophyta) the zone below. On the windward side only the calcareous green alga *Halimeda opuntia* (L.) Lamouroux, red *Laurencia papillosa* (Forsskål) Greville, and some of the *Oscillatoria* were found exposed.

A few specimens of the actinian *Stoichactis anemone* (Ellis) and barnacle *Tetraclita stalactifera* (Lamarck) were also encountered on the windward side. The most abundant crustaceans on the lagoon shore are the hermit crab *Clibanarius tricolor* (Gibbes), which clusters in great numbers on intertidal rock and rubble, and the elusive isopod *Ligia olfersii* Brandt, which is particularly common around empty conch shells near the concrete boat dock. Several crabs are common among rubble and concrete blocks all around the cay. *Grapsus grapsus* L. is the largest and most abundant; other crabs include *Pachygrapsus transversus* (Gibbes), *Cyclograpsus integer* Milne Edwards, and *Petrolisthes quadratus* Benedict. Among the mollusks only gastropods occur intertidally at Carrie Bow Cay. On the windward side *Nerita peloronta* L., *N. versicolor* (Gmelin), *Littorina nebulosa* Lamarck, *L. ziczac* (Gmelin) (Figure 54b), and *Tectarius muricatus* (L.) are found on vertical coral rock and concrete block surfaces of the seawall. Several size classes of juvenile *Cittarium pica* (L.) cluster among rubble or on beach rock below. *Nerita versicolor*, *L. ziczac*, and *T. muricatus* also occur on the leeward seawall but are less abundant there. A few specimens of a single species of echinoderm, the echinoid *Echinometra viridis* Agassiz, are found here and there under tide-exposed rocks.

### Climatic Parameters

The climate of Belize is subtropical to tropical, with temperatures ranging from 10° to 36° C (average range in Belize City, 23°–33° C), and rainfall averaging 125–450 cm a year. Temperatures are lowest in the highlands and during the cool period of the year (November to March). Average rainfall increases from north to south; the rainy season lasts from June to October. The overall climate of the country, particularly of the outer cays, is influenced by northeasterly trade



FIGURE 54.—Intertidal organisms; a, algae *Cladophoropsis* and *Oscillatoria* (top), *Neomeris* and *Padina* (bottom) on concrete block seawall; b, gastropod *Littorina ziczac* on coral boulder. (Picture width, a = 70 cm; b = 5 cm.)

winds that prevail at velocities of 4–5 m/s during about 70% of the year. Our meteorological records from Carrie Bow Cay, although not continuous, indicate major patterns of temperatures, solar radiation and cloudiness, wind, and rainfall and allow some comparisons with conditions prevailing on the mainland. In addition, 12-day continuous measurements of radiation, evaporation, wind, and air-water-sand temperatures in June 1975 were reported by Kjerfve (1978).

**TEMPERATURE AND SOLAR RADIATION.**—Figure 55 presents monthly temperature records, except for July and December. Data for January, February, and August to October are the result of a single year's readings; other data were derived from at least three consecutive years of observation. Values are plotted against a background of ten-year average minimum and maximum temperature readings provided by the Melinda Forest Station near Dangriga, on the mainland of Belize. Temperature conditions on the cay follow closely those on land, where the highest averages occur during May and August (33° C) and the lowest

during January and February (22° C, 21° C). Solar radiation measurements are only available for the cay and for the months of March through June, and November. The highest total radiation reaching the ground on a single day was recorded during April and May and amounted to 490 cal/cm<sup>2</sup>. Monthly averages of daily radiation related to this value give an indication of cloudiness and haze (Figure 55).

**WIND.**—Measurements of wind direction, speed, and frequency on Carrie Bow Cay are summarized in Figures 56 and 57. Values for March–June show the typical situation: northeasterly trade winds predominate and compare well with published wind roses from the open ocean surface off Belize (United States Naval Oceanographic Office, 1963). Our observations on wind for the rest of the year are sparse and may not be representative of long-term averages. Speed values for the infrequent winds from the northwest sector are somewhat low because of the shading effect of the big house and of coconut trees.

**RAINFALL AND HUMIDITY.**—Long-term rainfall

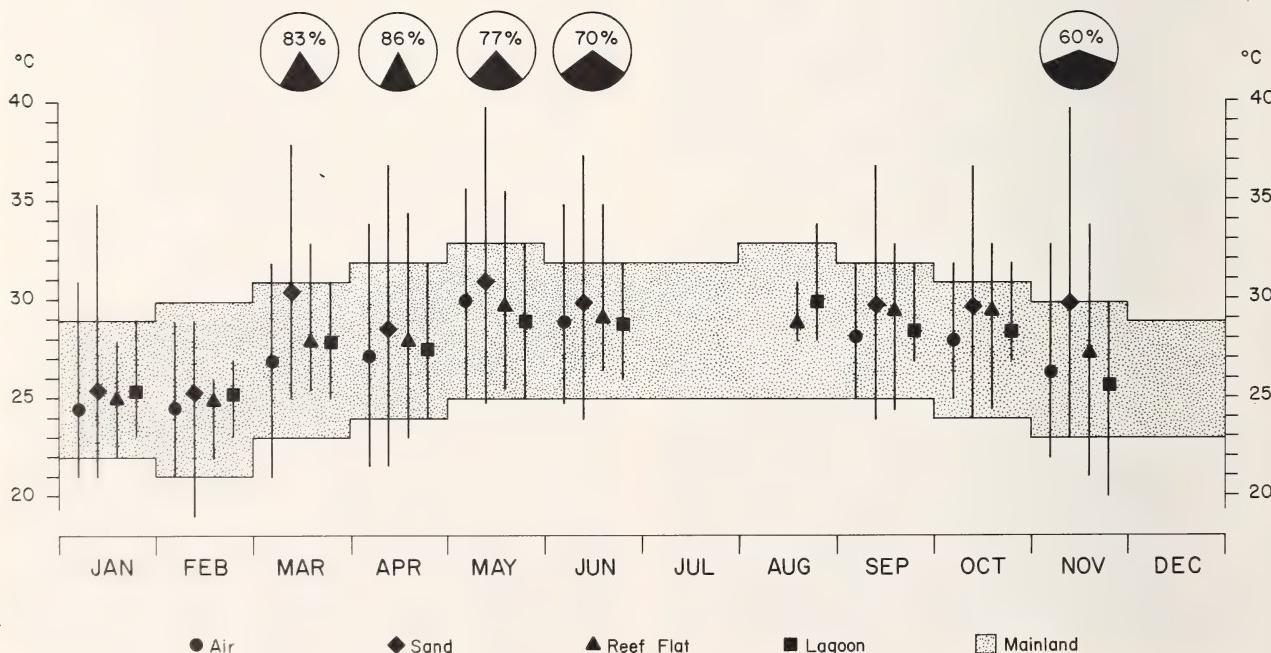


FIGURE 55.—Monthly temperatures (mean, range) 1976–1980 and solar radiation (percentage of maximum) 1978–1980 for Carrie Bow Cay; monthly temperature range (shaded area) at Melinda Forest Station on mainland, averaged over a ten-year period, 1965–1975.

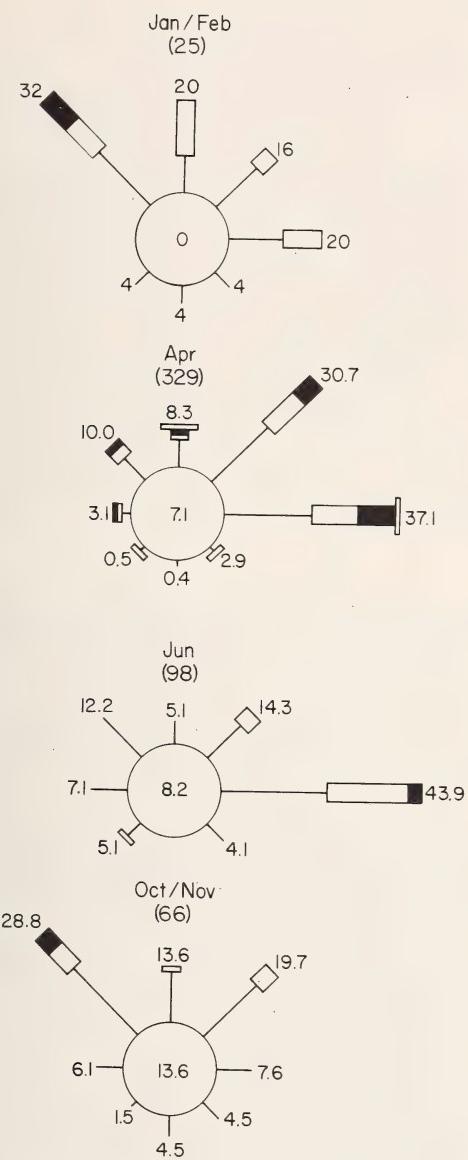
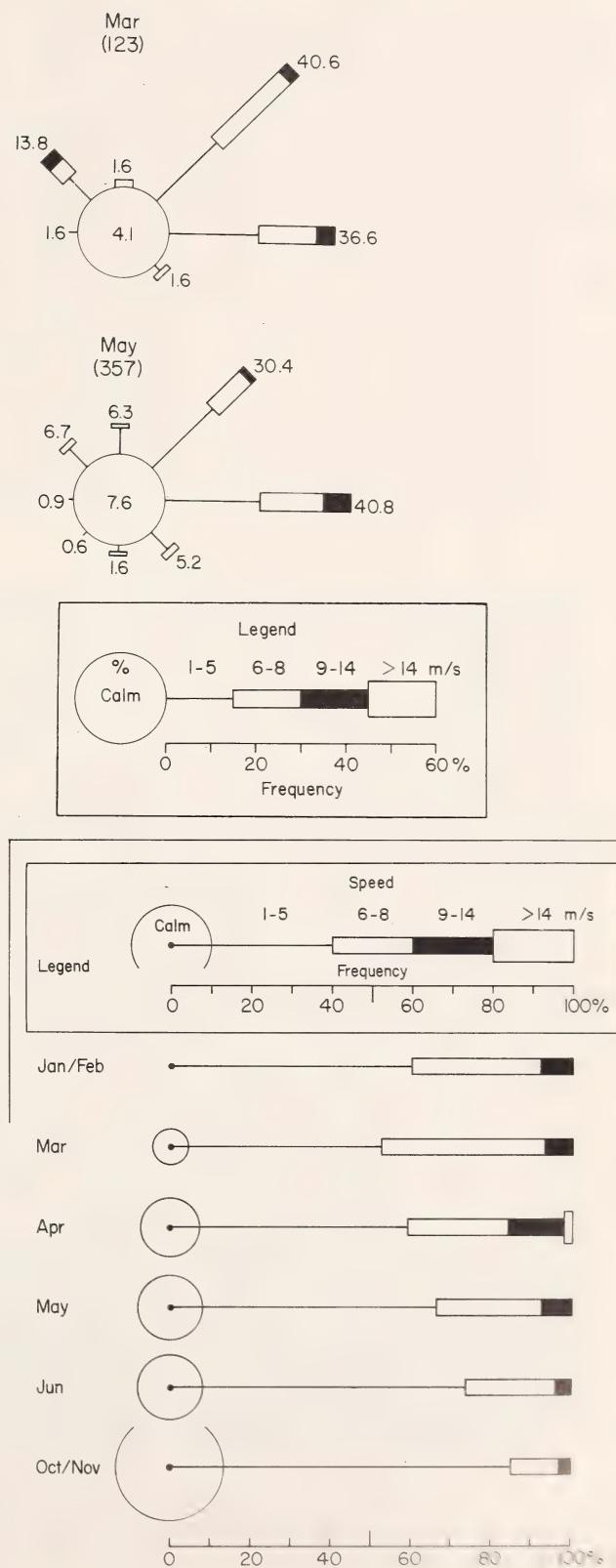


FIGURE 56 (above).—Wind roses for Carrie Bow Cay indicating direction, speed, and frequency (figures in parentheses are numbers of observations during 1976–1980).

FIGURE 57 (right).—Monthly summaries of wind speed frequencies during 1976–1980, Carrie Bow Cay.

data taken at the Melinda Forest Station indicate an average annual accumulation of 218 cm for the Dangriga district. The range is from 4.4 cm in March to 30.4 cm in September. Values for Carrie Bow Cay are presented in Figure 58 and compared with the mainland averages. The is-



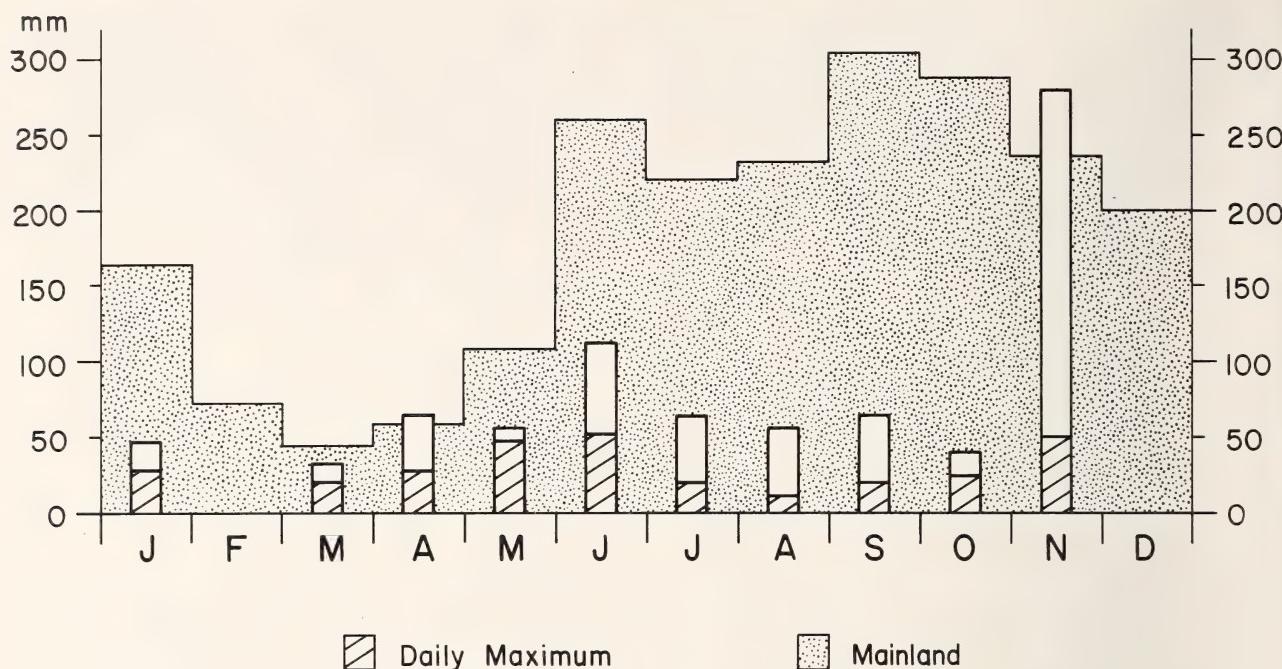


FIGURE 58.—Monthly average (total bar) and daily maximum rainfall on Carrie Bow Cay (1976–1980), compared with mainland monthly rainfall (Melinda Forest Station) averaged over a 71-year period (1906–1977).

land receives, on the average, only 42 percent of the mainland rainfall if one excludes February and December for which comparative data are lacking. The high value (279 mm) for November may be a peculiarity of the year (1979) in which the record was taken. On the other hand, a second but incomplete measurement of 213 mm (1978, November 14–26) indicates a similarly high or even higher rainfall during that month.

Humidity measured between March and June averaged 78 percent, with a range of 58–96 percent.

### Recent Hurricane Effects on Carrie Bow Cay

Computer files of the United States National Hurricane Center (P. J. Hebert, pers. comm.) indicate that at least 20 hurricanes and 45 tropical cyclones have passed within 100 nautical miles (185 km) of Belize City ( $17^{\circ}30'N$ ,  $88^{\circ}18'W$ ) during the last century (records date back to November 1889). From these data it can be determined that nine hurricanes and seven tropical storms

have passed Carrie Bow Cay within a 50 km radius. Storm activity in this area seems to have increased recently as six of the hurricanes and the most violent of tropical storms (Laura) have occurred within the last 20 years (Table 8).

Hattie is the only storm for which the long-term effects on Belizean reefs and cays, including Carrie Bow Cay, have been monitored (Stoddart,

TABLE 8.—Hurricanes passing within 50 km radius of Carrie Bow Cay, 1960–1980, including name, date, and maximum sustained wind speed while storm center was within 50 km of Carrie Bow Cay

Name	Month/Year	Wind speed (km/h)
Abby	Jul 1960	128
Anna	Jul 1961	148
Hattie	Oct 1961	259
Francelia	Aug 1969	182
Laura*	Nov 1971	111
Fifi	Sep 1974	176
Greta	Sep 1978	176

\* Officially declared a tropical storm.

1963, 1969, 1974). Other recent hurricane reports include a brief eyewitness account of tropical cyclone Laura passing over Glover's Reef and Stann Creek (Dangriga) (Antonius, 1972), and observations on the impact of hurricane Greta on the reef community near Carrie Bow Cay (Highsmith et al., 1980).

**HURICANE FIFI (14–22 September 1974).**—A tropical depression south of Puerto Rico and Hispaniola moving westward developed into hurricane Fifi on 17 September. Fifi, as reported by Hope (1975), acquired its maximum sustained winds of 95 kt (176 km/h) while it moved along the coast of Honduras, 18–19 September, where heavy rains caused a high number of deaths by

inland flooding of rivers. The hurricane crossed the barrier reef approximately 20 km south of Carrie Bow Cay and reached the coast of southern Belize during the afternoon of 19 September.

Our observations on the effects of Fifi on Carrie Bow Cay rely on a survey in December 1974 as no eyewitness reports are available. Storm surge flooded the entire island, and most of the unconsolidated sand was either piled up high inside the buildings or carried away, leaving a surface of coral rubble and exposed palm tree roots. A comparison of photographs (Figure 59) and a map of Carrie Bow Cay prepared by D. R. Stoddart in 1972 (Figure 60a) indicate that coastal erosion was strongest to the north, northeast, and



FIGURE 59.—Carrie Bow Cay silhouettes looking east: *a*, February 1972; *b*, December 1974, three months after hurricane Fifi. Note reduction of island size, in number of trees, and density of leaves caused by the hurricane.

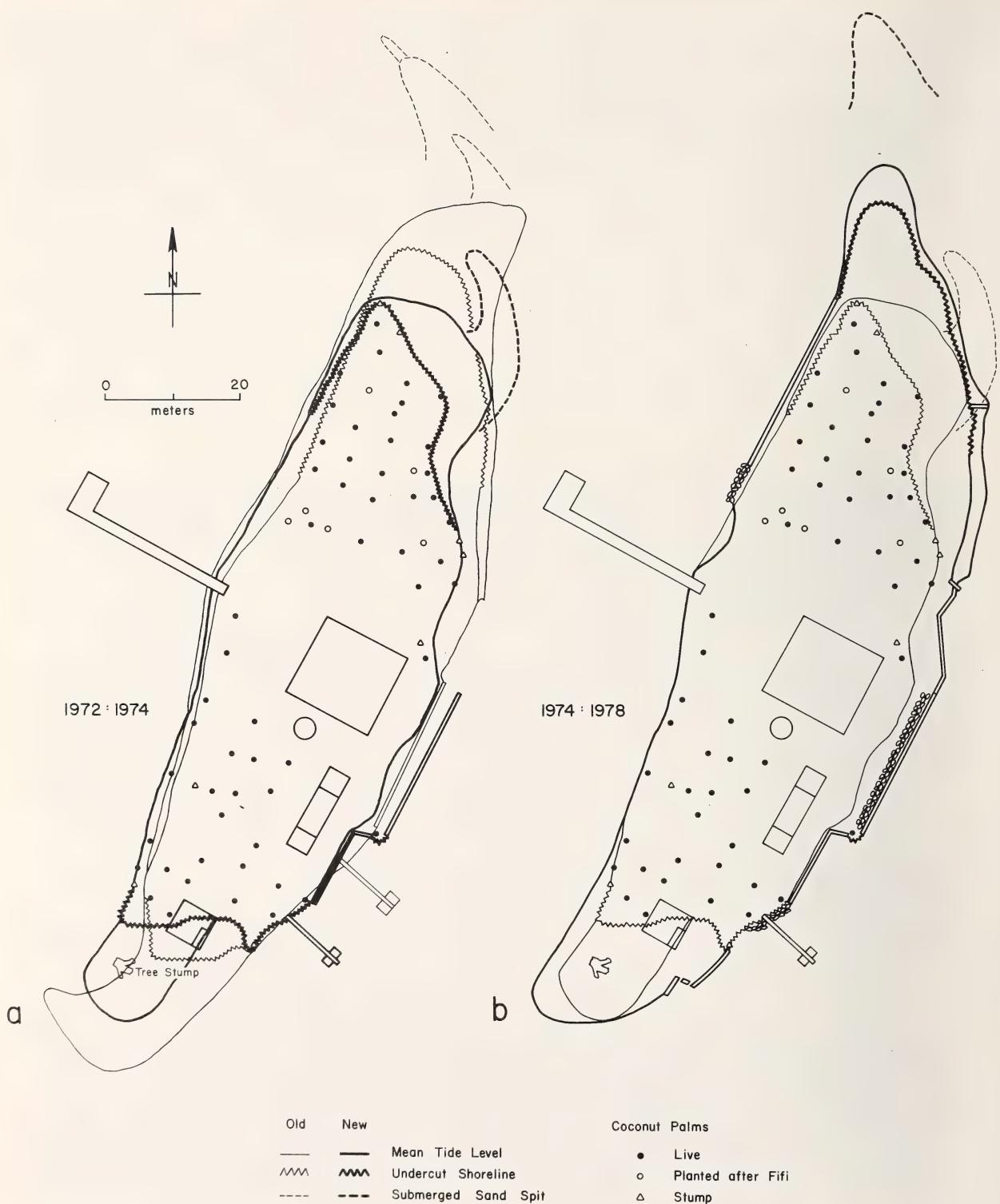


FIGURE 60.—Maps of Carrie Bow Cay showing hurricane effects and poststorm recovery: *a*, changes 1972-1974, caused principally by hurricane Fifi, September 1974; *b*, recovery, December 1974 to May 1978.



FIGURE 61.—Effects of hurricane Fifi: *a*, eroded north point of Carrie Bow Cay with fallen coconut palms, looking northeast; *b*, submerged bank of sand originating from northern portion of the island, looking northwest.

south of the island. About 30% of the island's surface area was lost, but some of it was regained by subsequent deposition along the western shoreline. Most island sand, however, settled as a subtidal sand bank to the northwest of the cay (Figure 61b). The eastern seawall and outhouse dock were destroyed and a huge tree stump, situated for years on the reef flat to the east, was floated to the new south tip of the cay. At least 14 coconut trees, predominantly from the north point and northeast shore were uprooted by erosion and either fell in place (Figure 61a) or were carried into the lagoon and sank. Others lost their tops in the storm or withered from overexposure to salt water. All other plants previously recorded (Stoddart, 1969), such as low *Tournefortia* bushes, *Euphorbia*, *Ipomoea*, and *Sesuvium* ground cover, and grasses, disappeared and did not recover to the approximate prehurricane condition until spring 1978. By that time, with the help of seawalls and rubble fills, much of the prehurricane island outline was restored (Figure 60b).

**HURRICANE GRETA** (13–23 September 1978).—The track of Greta was almost identical to that of Fifi, and both storms occurred at almost the same time in September. The meteorological history of Greta is described by Lawrence (1979). A depression formed northwest of Trinidad on 13 September. Hurricane force with sustained winds of 115 kt (213 km/h) developed at a position south of Jamaica on 16 September. Moving over the Bay Islands off the north coast of Honduras, Greta weakened and made its landfall with 80 kt (148 km/h) winds near Dangriga on the evening of 19 September. Greta was a much more severe hurricane than Fifi but despite locally heavy rain it did not cause devastating river floods (P. J. Hebert, pers. comm.).

The eye of hurricane Greta passed Carrie Bow Cay about 6 km to the north and brought the island winds of approximately 95 kt (176 km/h). Although direct observations are lacking, a considerable storm tide (about two meters above normal, estimated from events at Dangriga) must have flooded the island because the smallest cottage disappeared and the ocean-side wall of the

laboratory caved in. Despite damage to buildings, coastal erosion was considerably lower than during Fifi. About 20 coconut trees were lost, most of these from the leeward side of the island. Other plants were much less affected by Greta than by the 1974 hurricane as only one common and four minor species disappeared (Table 7).

## Summary and Conclusions

From its position, structure, and flora, Carrie Bow Cay can be classified as a reef-derived sand cay. It is located at the seaward margin of the barrier reef, is composed of reef rubble and sand, and is held together primarily by coconut rootlets and, to a lesser degree, by ground cover and artificial structures. The island measured a little over two acres (0.8 ha) when it was bought by the present owners in 1943. Today it is less than half that size and exposed beachrock on the windward side indicates westward (leeward) migration, which confirms the view that sand cays of this nature are slowly migrating sand waves (Miliman, 1973).

Because of its small size, low elevation, and porous substrate, Carrie Bow Cay lacks a fresh-water lens and it has not developed a complex terrestrial environment. Considering the occasional salt water flooding during storm tides, the island may be described as a supralittoral habitat. The climate, too, is dominated by the surrounding ocean and by northeasterly trade winds; it is moderate in comparison with the nearest mainland.

Clearing of vegetation during this century and increased hurricane activity in the area during the past two decades are mainly responsible for the rapid shrinking of Carrie Bow Cay. Captain Owen, who mapped the island as "Jack Ellin's Cay" in 1830, noted "tops of bushes 20 feet" (Stoddart, 1963), presumably seagrape, baycedar, and mangrove. Coconuts planted in the early 1900s, and repeatedly again since, may not be equally effective in holding the sand, also, they do not protrude into the intertidal to trap sediments or break the power of waves or currents.

Although physiographic change of the cay was minor during hurricane Hattie (Stoddart, 1963, 1969), later storms, Fifi in particular, took severe toll. Recovery of plant cover destroyed by Fifi took about four years. Colonization of sand cays is thought to be primarily by floating seeds or by seeds carried by birds (Stoddart, 1960), or by wind, but direct observations on these processes are sparse. Possible means of dispersal judged from seed type are listed in Table 7 (data pro-

vided by M.-H. Sachet). Our own findings suggest that only four of 16 species of plants—coconut, red mangrove, and two unidentified seedlings—arrived by sea and sprouted. None of them survived beyond two years because of the unsuitable location of settlement. Experimental studies on natural means of island colonization should be the next step in elucidating the terrestrial development of Carrie Bow Cay.

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# Distribution of Microborers within Planted Substrates along a Barrier Reef Transect, Carrie Bow Cay, Belize

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and Ronald D. Perkins

## ABSTRACT

A diverse assemblage of endolithic microorganisms was identified in a series of carbonate substrate stations planted along a transect across the barrier reef near Carrie Bow Cay, Belize. These tropical endoliths at the sediment-water interface include the cyanophytes, *Hyella tenuior* Bornet and Flahault, *Mastigocoleus testarum* Lagerheim, and *Plectonema terebrans* Bornet and Flahault, the chlorophytes, *Ostreobium brabantum* Weber Van-Bosse and *Phaeophila engleri* Reinke, the rhodophyte *Porphyra* sp. (*Conchocelis*-phase), and various fungi. This assemblage was subdivided into an upper photic zone assemblage dominated by *Mastigocoleus*, *Hyella*, *Phaeophila*, and *Ostreobium* species, and a lower photic zone assemblage dominated by *Porphyra* sp.

Subsurface endolithic activity detected at the shallow lagoon station included filamentous irregular polygonal networks, irregular flattened masses, and regular crenulate discoids, which differed from and were less diverse than the assemblage at the sediment-water interface. Affinities of these subsurface microborings are unknown but they resemble endolithic traces and organic scars variously attributed to fungi, bacteria, and Actinomycetes. The regular discoids and irregular masses occurred only in association with the filamentous form, and therefore may be related reproductive bodies. For reasons not fully under-

stood, microborings were not present in the second subsurface station, in fore-reef sand at a depth of 24 m.

## Introduction

Endoliths are microorganisms (generally less than 1  $\mu\text{m}$  to 100  $\mu\text{m}$  in diameter) that penetrate calcareous substrates by chemical and/or mechanical means and that leave post-mortem microscopic networks. They are distinguished from "epiliths," which live only on a substrate's surface, and from "chasmoliths," which adhere to surfaces of fissures or cavities within the substrate (Golubic et al., 1975). Endoliths include cyanophytes, chlorophytes, rhodophytes, fungi, and possibly bacteria and sponges.

The most diverse and ecologically important microborers occur in the marine setting; their boring patterns—size, mode of branching, spatial arrangement, and growth directions—are taxonomically characteristic (Golubic, 1972). The marine endoliths have been subdivided on the basis of bathymetric and regional assemblage distributions, which are controlled by geographic, climatic, photic, and environmental factors (Perkins and Halsey, 1971; Perkins, 1972; Rooney and Perkins, 1972; Golubic et al., 1975; Green, 1975). Various studies of ancient and modern forms have indicated that endoliths may be used to interpret paleoclimatic conditions and to recon-

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struct depositional environments (for example, see Swinchatt, 1965; Gatrall and Golubic, 1970; Perkins and Tsentas, 1976). As well, microboring organisms have been used to establish the positions of relict shorelines (Perkins and Halsey, 1971; Edwards and Perkins, 1974) and to detect sediment transport (Rooney and Perkins, 1972).

Microborers modify both lithified and unlithified carbonate coasts (Purdy and Kornicker, 1958; Hodgkin, 1970; Schneider, 1976), in the colonization of shifting upper sublittoral substrates—where they create finer carbonate sediments, preferentially remove certain components, and initiate micrite rind formation (Bathurst, 1966; Golubic, 1969; Alexandersson, 1972; Rooney and Perkins, 1972; Perkins and Tsentas, 1976)—and in their alteration of the deep-sea sedimentary record (Zeff and Perkins, 1979). Endolithic algae not only dissolve carbonates, but also induce precipitation of calcium carbonate within shallow marine corals (Schroeder and Ginsburg, 1971; Schroeder, 1972a, b; Scherer, 1974). Furthermore, their biologically related physico-chemical processes may influence low-temperature sedimentary mineralization within boring networks (Taylor, 1971; Kobluk and Risk, 1977).

Recently, planted substrates have been used to identify modern microboring assemblages and to establish rates of infestation (Golubic, 1969; LeCampion-Alsumard, 1975; Perkins and Tsentas, 1976). The present investigation examined and identified endoliths within planted substrates in order to determine the distributional patterns of these organisms at the sediment-water interface along a reef transect. Two stations planted below the sediment surface allowed a cursory examination of subsurface microboring activity.

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## Methods

This study examined two types of carbonate substrates planted at and below the sediment-water interface along a reef transect of Carrie Bow Cay (Figure 62): (1) crushed, fresh inner shell parts of the queen conch, *Strombus gigas* Linnaeus, and (2) cleaved calcite rhombohedra. Samples of each type were retained as controls. Fragments from 1 to 10 mm in size were attached to 15 cm<sup>2</sup> plexiglass plates (one type per plate) and 40 cm long polyvinyl chloride (PVC) pipes (types mixed) by a thin film of epoxy resin. Fourteen substrate-covered plexiglass plates were mounted on short lengths of protruding PVC pipe to maintain the samples above shifting substrata (Figure 63). These plates were placed in pairs at seven locations extending from the lagoonal *Thalassia* zone (depth 1.2 m) to the fore-reef slope (depth 27.4 m). One subsurface pipe station (consisting of one pipe) was inserted into the sea floor in the *Thalassia* zone (Figure 64) and another into the *Halimeda*-rich sand of the fore-reef sand trough (depth 24 m). Exposure time of substrates ranged from 21 to 24 months.

After being harvested, the planted substrates were preserved in 4 percent formaldehyde in 0.1 M phosphate neutral buffer. Fragments intended for light microscopic study were carefully scraped to remove epilithic organisms, then dissolved with 5 percent EDTA solution (van Reine and van den Hoek, 1966) at a pH of 6. Although the three-dimensional configuration of the microborers is lost because of their collapse, organic structure and color are not damaged by this slow-dissolving solution. Extracted tissues were then mounted on glass slides.

Scanning electron microscopic (SEM) analysis was based on the casting-embedding technique of Golubic et al. (1970). An alcohol dehydration series was followed by an infiltration series using Durcupan ACM Araldite Base Embedding Agent. After polymerization within plastic holders, the substrate fragments were exposed by means of a rotary grinding tool, then etched with 3 percent hydrochloric acid. This technique revealed plastic casts of the microboring networks,

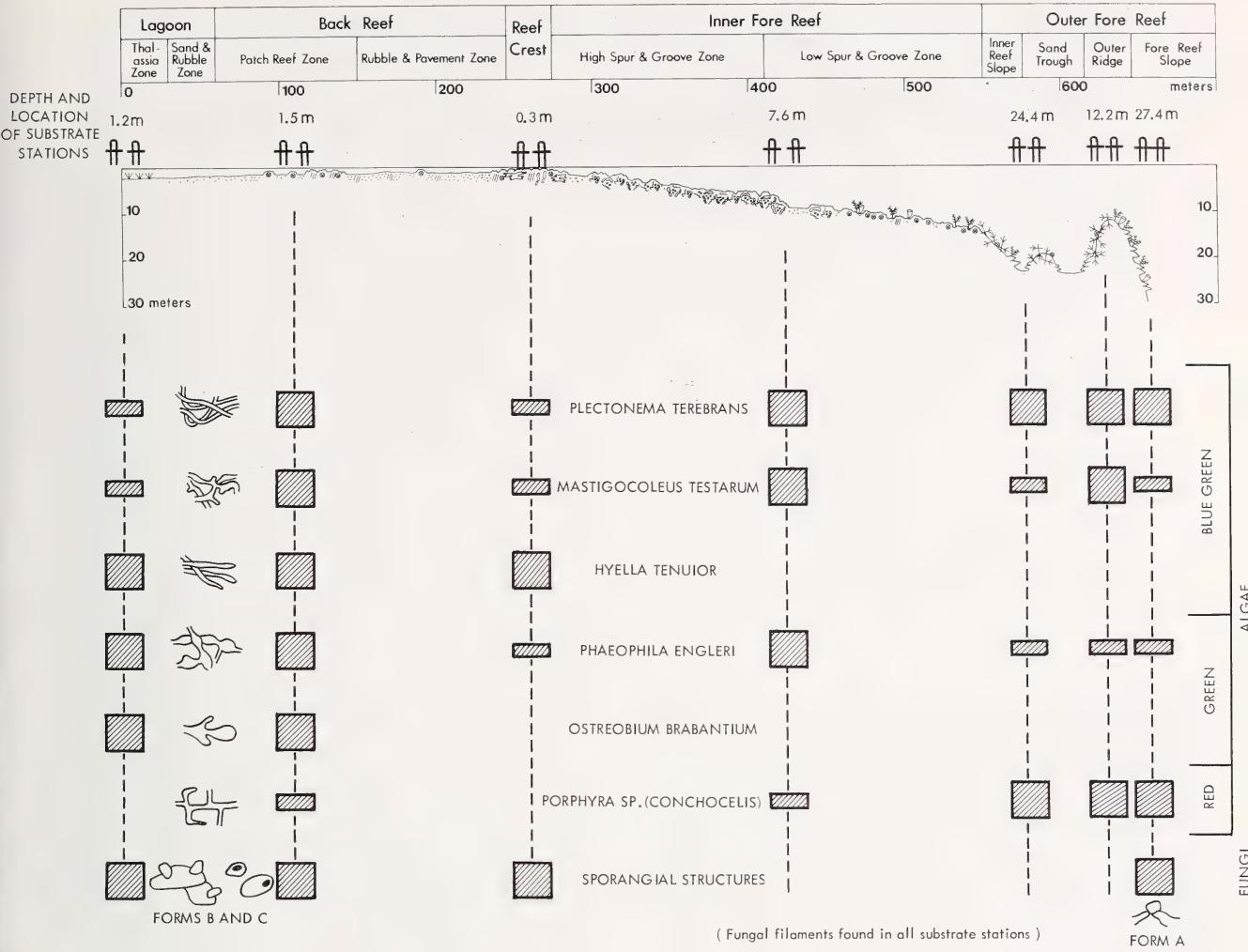


FIGURE 62.—Idealized cross section of Carrie Bow Cay transect showing locations of substrate stations planted at sediment-water interface and the distribution of endoliths collected from these plates (hatched squares = great abundance; hatched rectangles = presence observed).

which retained the original spatial relationships of the endoliths and their three-dimensional configurations. The mounted plastic blocks were scanned with an International Scientific Instruments Super II electron microscope after vacuum shadowing with gold-palladium alloy. Casts of boring networks were correlated with the endoliths isolated by acid dissolution.

## Results

**ENDOLITHS AT THE SEDIMENT-WATER INTERFACE.**—Blue-green algae were ubiquitous and

consisted of *Hyella tenuior* Bornet and Flahault, *Mastigocoleus testarum* Lagerheim, and *Plectonema terebrans* Bornet and Flahault. Green algal microborers, likewise abundant, included *Ostreobium brabantium* Weber Van-Bosse and *Phaeophila engleri* Reinke. Red algae were much less abundant and were represented only by the *Conchocelis*-stage of *Porphyra* sp. Fungal forms were found in almost all samples.

*Plectonema terebrans* was the most common cyanophyte at all stations. Diagnostic are its smooth, elongate, thread-like filaments 2 to 4  $\mu\text{m}$  in diameter, which may run along the interior



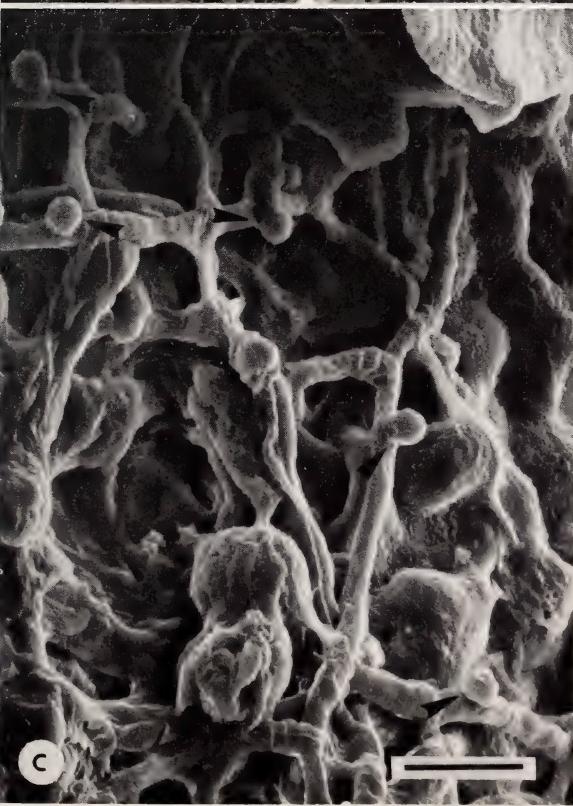
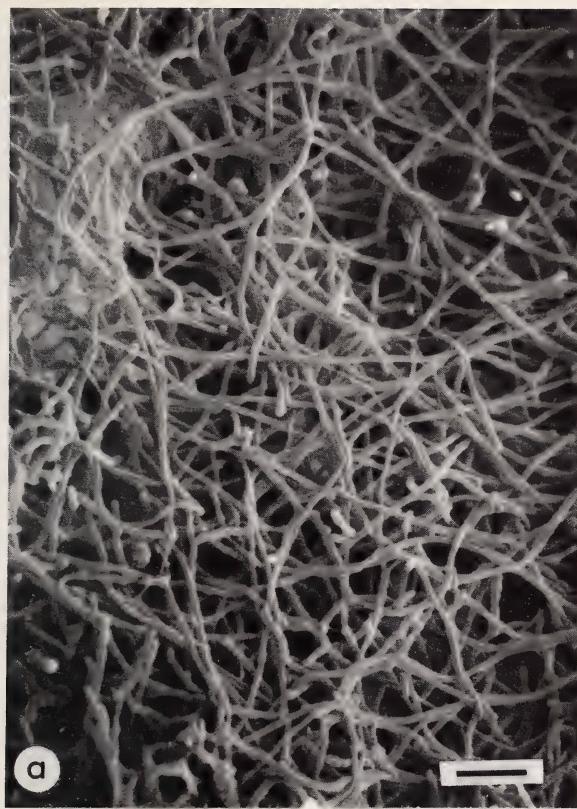
FIGURE 63.—Patch reef zone substrate station, Carrie Bow Cay, showing location of plates above the sediment-water interface.



FIGURE 64.—*Thalassia*-zone subsurface substrate station, Carrie Bow Cay, showing a closeup of the buried substrate-covered 40 cm long PVC pipe. Note that only the protective collar and a small portion of the pipe protrude above the sediment-water interface.

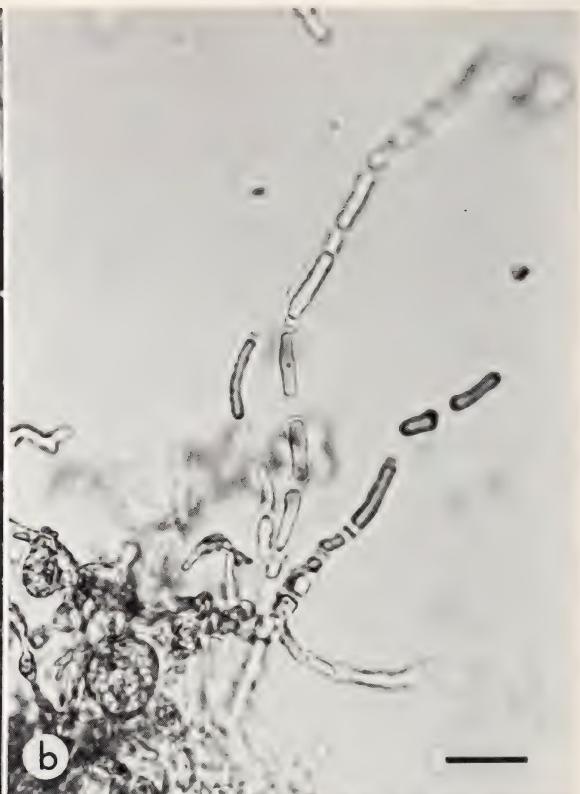
surface of the substrate or may form dense, interwoven meshworks (Figure 65a,b). Also ubiquitous was *Mastigocoleus testarum*, which is composed of sharply curved to elongate filaments 5 to 8  $\mu\text{m}$  in diameter that have numerous short lateral branches and heterocysts (Figure 65c,d). The morphology of *M. testarum* penetrating inorganic substrates is much more affected by the rhombohedral microstructure than is the morphology of *P. terebrans*; this observation corresponds with findings of LeCampion-Alsumard (1975). *Hyella tenuior*, which is less common, appears as a cluster of slender, elongate, relatively straight to bent filaments 5 to 8  $\mu\text{m}$  in diameter (Figure 66a,b). These filaments grow subperpendicular to the surface of the substrate.

FIGURE 65.—Scanning electron and transmitted light photomicrographs of endolithic algae: a, *Plectonema terebrans* forming a typical dense network of filaments, acid-etched mollusk fragment, *Thalassia* zone (note the smooth, elongate, fine nature of the plastic casts); b, *P. terebrans* isolated by dissolution of a mollusk fragment, reef-crest zone; c, characteristic heterocyst development of *Mastigocoleus testarum* shown on plastic casts, acid-etched mollusk fragment, *Thalassia* zone; d, *M. testarum* isolated by dissolution of a mollusk fragment, *Thalassia* zone (note the heterocyst development marked by arrows). (Scale = 50  $\mu\text{m}$  for a, d; 40  $\mu\text{m}$  for b; 25  $\mu\text{m}$  for c.)

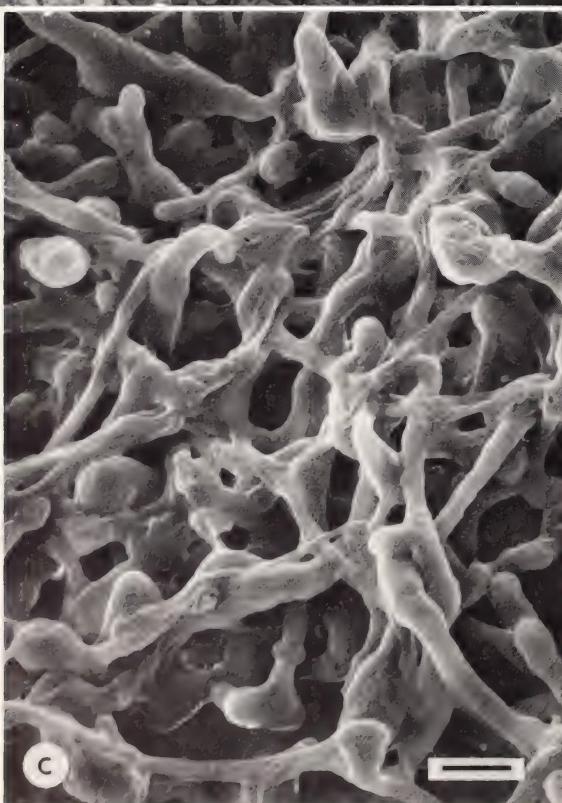




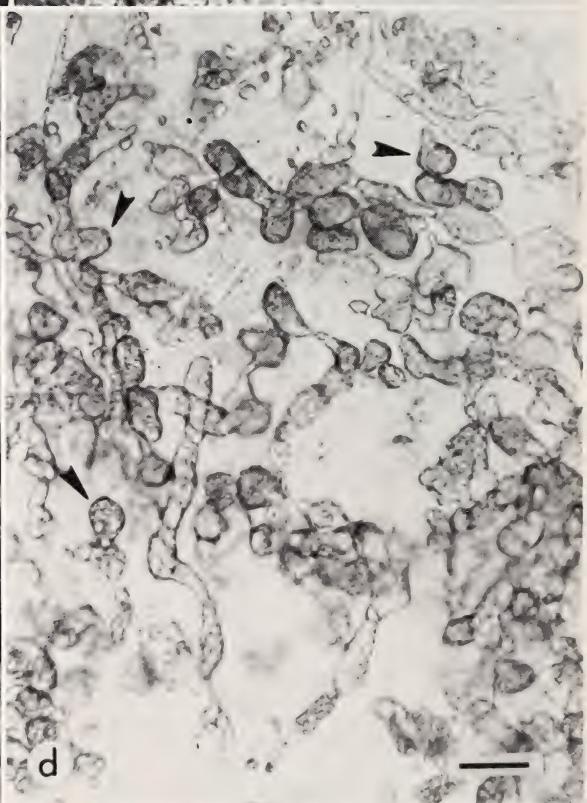
a



b



c



d

*Phaeophila engleri* was the most abundant and widespread chlorophyte. This species is characterized by rectilinear branching and pronounced bulbous or irregularly ovoid, 15 to 20  $\mu\text{m}$  swellings at points of branching or along the irregular 5 to 10  $\mu\text{m}$  filaments (Figure 66c,d). The largest boring species detected, *Ostreobium brabantum* has digitate growths of single or bilobate branches (Figure 67a,b). Single plants up to 1 mm in length radiate into the substrate; individual branches of 40 to 60  $\mu\text{m}$  may enlarge up to 120  $\mu\text{m}$  before bifurcation. The *Conchocelis*-stage of the rhodophyte *Porphyra* sp. is characterized by rectilinear branching of long and fine, 2 to 3  $\mu\text{m}$  filaments running along slightly beneath the substrate surface (Figure 67c,d).

Extremely fine filaments from less than 1 up to 4  $\mu\text{m}$  in diameter occur in a wide variety of forms, from non-branched to extensively branched and fused, sparse to massive networks (Figure 68a,b). These filaments probably represent fungal hyphae. The hyphae appear to be directed towards algae and can be observed penetrating these organisms, presumably in the act of feeding (Figure 68b). Three different types of structures observed with the scanning electron microscope were attributed to fungal spore cases. Form A has 5 to 15  $\mu\text{m}$  ovoid to pyriform reproductive bodies, from the bases of which radiate long and thread-like, 1 to 2  $\mu\text{m}$  hyphae (Figure 69a). These hyphae are typically unbranched and connect spore cases. Form B has 8 to 20  $\mu\text{m}$ , globose to oblong fruiting bodies with connective hyphae attached at their

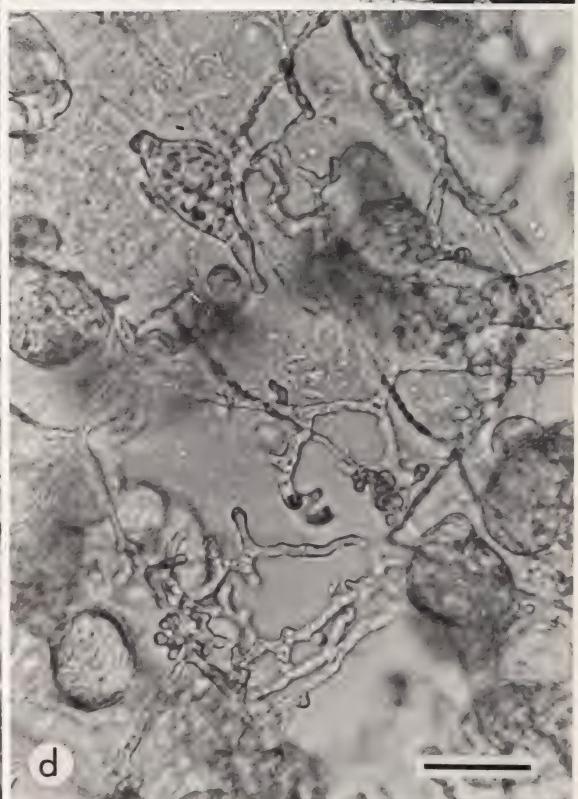
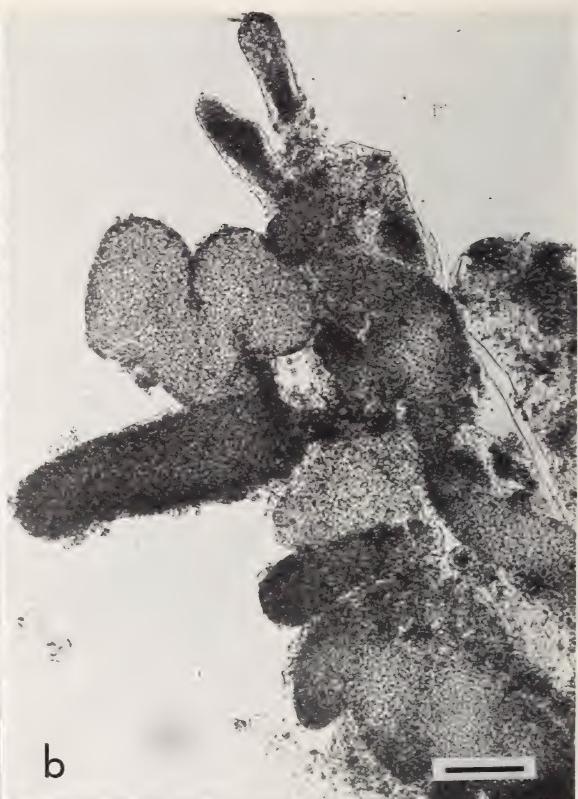
FIGURE 66.—Scanning electron and transmitted light photomicrographs of endolithic algae: a, elongate casts of the blue-green alga *Hyella tenuior* directed away from the substrate surface, some branching near their bases, plastic cast within an acid-etched calcite rhomb, *Thalassia* zone (very little control is exerted by the substrate microstructure); b, filaments of *H. tenuior* displaying elongate, somewhat rectangular cells, isolated by dissolution of the molluscan substrate, *Thalassia* zone; c, green alga *Phaeophila engleri* exhibiting characteristic ovoid swelling at points of branching and rectangular branching pattern, plastic cast of etched mollusk fragment, *Thalassia* zone; d, *P. engleri* demonstrating probable sporangia (arrows) and swellings at branching points, filaments isolated by dissolution of a molluscan substrate, *Thalassia* zone. (Scale = 50  $\mu\text{m}$  for a; 25  $\mu\text{m}$  for b, c; 40  $\mu\text{m}$  for d.)

sides, so that these spore cases appear positioned along filaments (Figure 69b). The irregular hyphae of less than 1  $\mu\text{m}$  diameter become branched and fused, and form interconnected networks. Fungal form C has 5 to 15  $\mu\text{m}$  globose to discoid sporangial bodies with indented ends that appear "doughnut-shaped" (Figure 68c). These bodies occur alone or in clusters directly upon the surface of endolithic algae; connective hyphae are lacking.

ENDOLITHS BELOW THE SEDIMENT-WATER INTERFACE.—In contrast to the diverse assemblage of microorganisms boring into the substrates planted at the sediment-water interface, only a few endolithic forms were found below the surface. These boring organisms were present only in the molluscan fragments planted within the lagoonal *Thalassia* zone. Classification is problematic as these forms have not previously been described. No microboring activity was recorded at the subsurface station in the fore-reef sandtrough zone.

An extremely irregular, polygonal network of variable and intermittent filaments 5 to 7  $\mu\text{m}$  in diameter (Figure 70a,b) commonly crosses the regular and parallel lines representing remnants of the organic matrix that separated the inorganic crystals of the gastropod shell. This network of variously spaced filaments bores just below the surface of the molluscan substrates. The filaments are curvilinear, have a twisted appearance, and branch sideways. This form is recurrent in approximately 10 percent of the molluscan fragments throughout the pipe planted in the *Thalassia* zone, and was not found in the control samples or in samples from the sediment-water interface. Possibilities for taxonomic assignment include marine fungi (Phycomycetes, Ascomycetes, and Deuteromycetes) and filamentous bacteria (Actinomycetes).

Another group occurs as regular patches or regular crenulate discs associated only with the irregular polygonal networks described above (Figure 70c,d). These may be reproductive structures or separate endolithic forms; they range from 125 to 200  $\mu\text{m}$  in diameter and average 2  $\mu\text{m}$  in thickness. Although they may be remnants



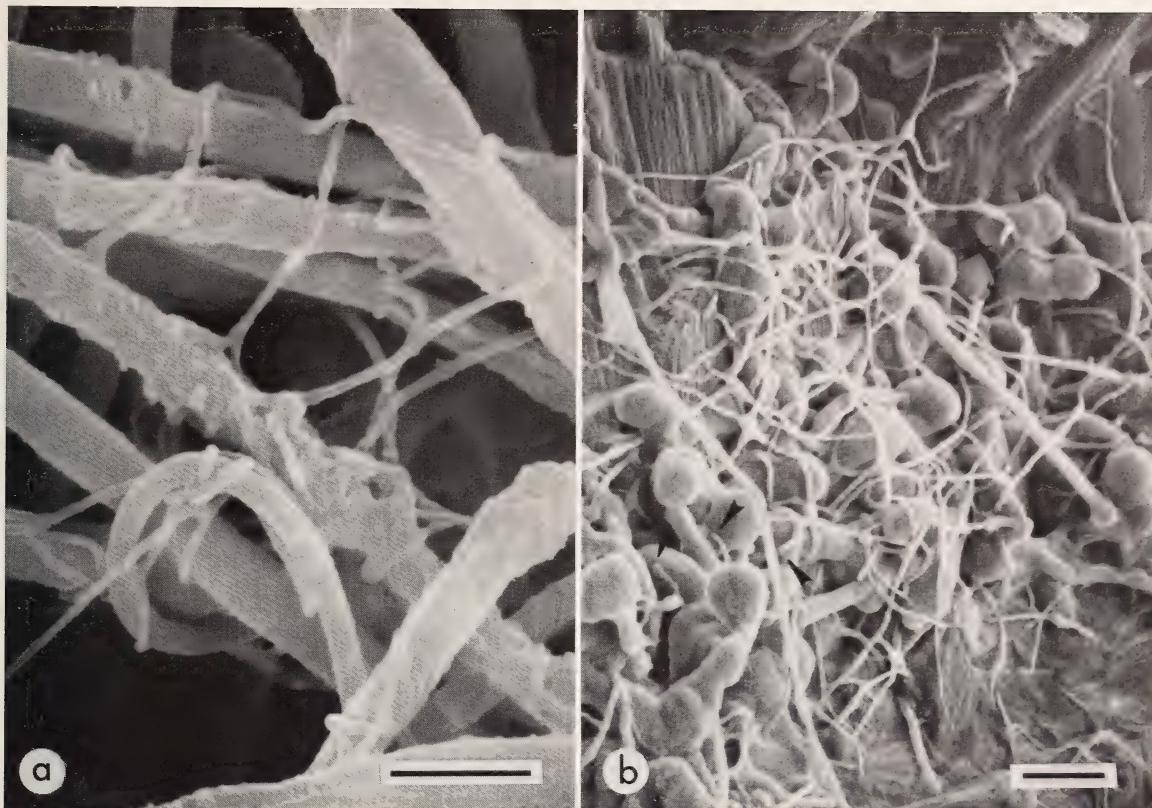


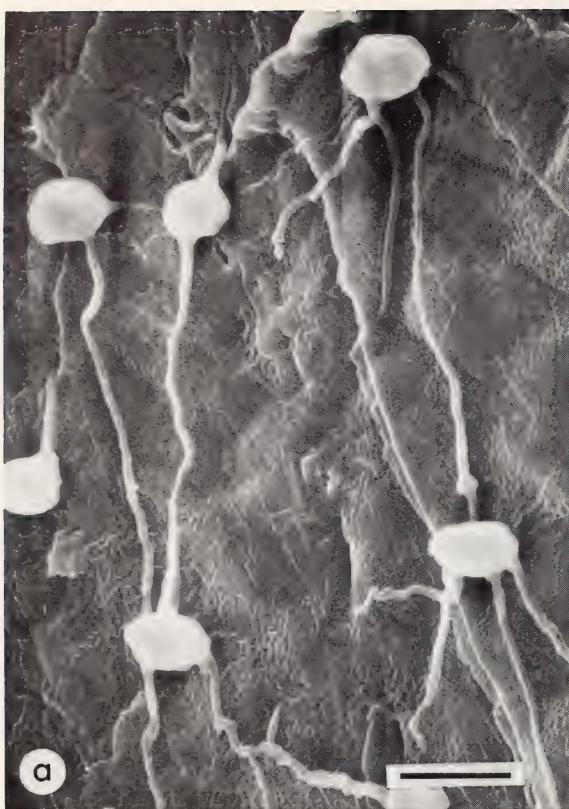
FIGURE 68.—Scanning electron photomicrographs of endolithic fungi: *a*, little-branched, thin plastic casts believed to be fungal hyphae, intertwined with the larger blue-green alga *Plectonema terebrans*, etched mollusk fragment, *Thalassia* zone; *b*, network of fine fungal borings covering and possibly feeding (arrows) upon the underlying alga, plastic casts within an etched mollusk substrate, *Thalassia* zone. (Scale = 5  $\mu\text{m}$  for *a*; 25  $\mu\text{m}$  for *b*.)

of the organic matrix, no analogous structures were found in any control sample or in any sample infested at the sediment-water interface.

FIGURE 67.—Scanning electron and transmitted light photomicrographs of endolithic algae; *a*, large, radiating growth form of the green alga *Ostreobium brabantum*, plastic cast within an acid-etched mollusk fragment, *Thalassia* zone (note both the single and bilobate branches, background forms are algae and fungi); *b*, *O. brabantum* filaments isolated by dissolution of a molluscan substrate, patch-reef zone; *c*, characteristic rectilinear pattern of the *Conchocelis*-stage of the red alga *Porphyra* sp., plastic cast, enhanced on a microscale by boring within a calcite rhomb, fore-reef slope zone (larger forms are an unidentified alga with strong microstructural control upon its boring pattern); *d*, *Conchocelis*-stage of *Porphyra* sp. displaying fine filaments in the typical rectilinear pattern, isolated by dissolution of a molluscan substrate, fore-reef slope zone. (Scale = 200  $\mu\text{m}$  for *a*; 100  $\mu\text{m}$  for *b*; 25  $\mu\text{m}$  for *c, d*.)

## Discussion

**ENDOLITHS AT THE SEDIMENT-WATER INTERFACE.**—The bathymetric distribution of Belizean endoliths was compared with similar tropical microbioring assemblages recovered from artificial substrate stations planted in reefs off St. Croix and Jamaica (Green, 1975; Perkins and Tsentas, 1976). The distribution of autotrophic endolithic organisms is related to light penetration in the sea—both the intensity of illumination and spectral composition (Golubic et al., 1975). Although endolithic organisms cannot be assigned to absolute depths—owing to variations in water clarity, currents, and other environmental factors—Perkins and Tsentas (1976) pointed out that “clear-water” assemblages might be used to estimate maximum depths for endolithic algae. Their di-



a



b



c

FIGURE 69.—Scanning electron photomicrographs of endolithic fungi: *a*, form A, characterized by ovoid to pyriform reproductive bodies, distributive unbranched casts of hyphae radiate from the base of the fruiting bodies just below the surface of the substrate, plastic cast of an etched calcite rhomb, fore-reef slope; *b*, reproductive bodies of fungal form B laterally connected by hyphae, etched mollusk fragment, *Thalassia* zone (these bodies are typically globose to oblong, note twisted or irregular appearance of the hyphal casts); *c*, "doughnut-shaped" or indented sporangial bodies of fungal form C, plastic cast in an etched mollusk substrate, *Thalassia* zone (note that these occur in close proximity to the outer substrate surface or to algal borings). (Scale = 10  $\mu\text{m}$  for *a*, *b*; 25  $\mu\text{m}$  for *c*.)

vision of such assemblages into an upper photic zone of *Mastigocoleus*, *Hyella*, *Phaeophila*, and *Ostreobium* species, and a lower zone dominated by *Porphyra* sp. in its *Conchocelis*-phase parallels, to some extent, the zonation found in the present study (Figure 62).

*Ostreobium brabantum* was observed only in the shallowest (1.2 and 1.5 m) sites of the *Thalassia* and patch-reef zones off Belize. In St. Croix, although present to 30 m, *O. brabantum* was predominant in depths less than 15 m (Perkins and Tsentas, 1976). Also, only the three shallowest sites off Belize contained *Hyella tenuior*, which was found down to 45 m in Jamaica (Green, 1975).

Four species of algae occurred at all depths along the Carrie Bow Cay transect. *Phaeophila engleri* was most abundant from 1.2 m to the 7.6 m spur and groove zone of the inner fore reef; similarly, this species is very common in the shallower zones of St. Croix and Jamaica. *Mastigocoleus testarum* was most abundant in the upper 12 m of the Belize sites, as was the case in St. Croix. Off Belize, however, it decreased slightly in the reef-crest and *Thalassia* zones. *Plectonema terebrans* was ubiquitous off Belize as well as Jamaica and St. Croix, except that in Belize it was less abundant in the *Thalassia* and reef-crest zones. Patchily distributed below 1.5 m, *Porphyra* sp. was most common in depths of 12 to 27 m, the deepest zone examined off Belize. This pattern has also been reported from the Australian Barrier Reef (Rooney and Perkins, 1972), the Puerto Rico shelf (Perkins, 1972), and Woods Hole, Massachusetts (Golubic et al., 1975), as well as Jamaica and St. Croix (Green, 1975; Perkins and Tsentas, 1976).

Although thin filaments believed to be fungal hyphae were present at all depths, the distribution of different sporangial structures was depth dependent. Fungal form A, with pyriform to ovoid bodies, from which basal hyphae radiate, was found only in the sample from 27 m on the fore-reef slope. Similarly, Perkins and Tsentas (1976) found a reticulate fungal form at 30 m in St. Croix. Forms B and C with laterally arranged globose spore cases and isolated "doughnut-

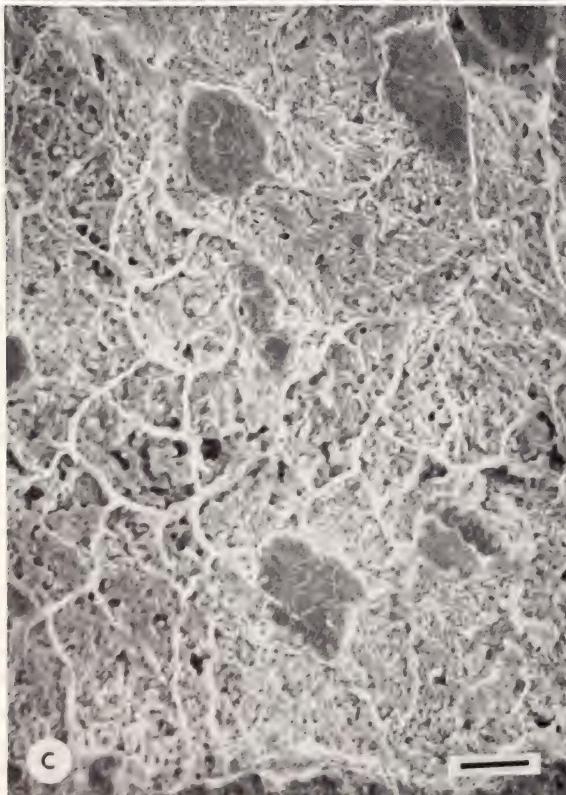
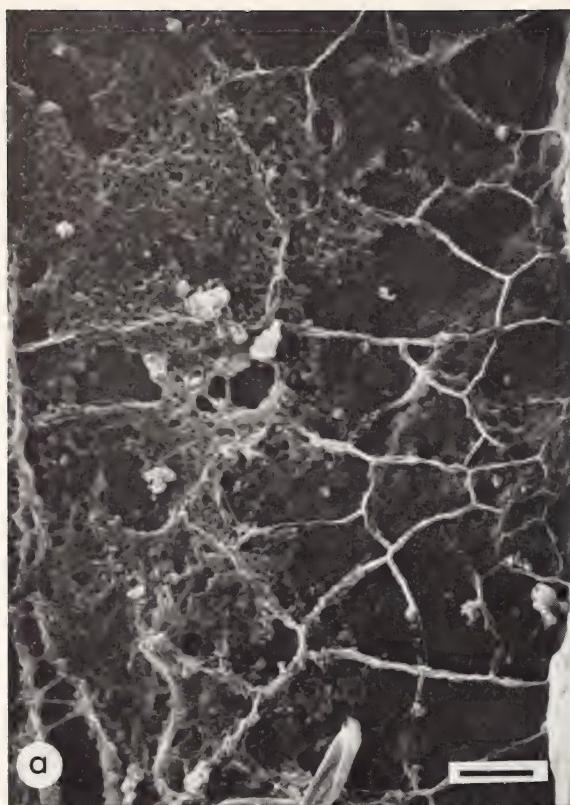
shaped" bodies, respectively, were found only in the shallow reef-crest, patch-reef, and *Thalassia* zones off Belize.

**ENDOLITHS BELOW THE SEDIMENT-WATER INTERFACE.**—Fungi may be as important as bacteria in breaking down organic matter into a nutrient source for other organisms. Marine fungi may be as versatile and potent in their feeding activity as their terrestrial and fresh-water counterparts, and are probably able to attack the entire spectrum of plant and animal detritus (Johnson and Sparrow, 1961). Endolithic fungi in living and dead shells at the sediment-water interface produce intertwined, anastomosing, and branched networks, and are able to use the energy contained in organic conchiolin and chitin matrix and to parasitize algal microborers (Kohlmeyer, 1969; Calvaliere and Alberte, 1970; Green, 1975; Zeff and Perkins, 1979).

Although marine fungi are generally believed to be restricted to the aerobic surface layers of bottom sediments, the Thraustochytriaceae and Chytridiaceae commonly occur well below the sediment surface (Clokie, 1970; Bremer, 1976; Johnson, 1976). The similarity between irregular polygonal networks observed in this study and microborings attributed to fungi leaves little doubt that these polygonal networks are of fungal origin.

The associated irregular masses and crenulate discoids may be the reproductive bodies of these boring fungi. Kohlmeyer (1969) described irregular black perithecia and conidia 100 to 125  $\mu\text{m}$  in diameter as fruiting bodies for endolithic marine Ascomycetes and Deuteromycetes. Alternatively, these masses may be separate endolithic fungal colonies, similar to irregular patches and to crenulate rosettes attributed to fungal colonies attacking spores, pollen, and other organic microfossils (Elsik, 1971).

In addition, two other groups of organisms, the bacteria and Actinomycetes, could produce endolithic scars resembling these forms. Similar scars on modern and ancient spores and pollen have also been attributed to bacteria and Actinomycetes (Moore, 1963; Elsik, 1966, 1971; Hav-



inga, 1971). Both groups are abundant at all levels within bottom sediments (ZoBell and Feltam, 1942) and at all depths sampled in lakes and the ocean (ZoBell and Rittenberg, 1938; Weyland, 1969; Willoughby, 1976). Boring by bacteria and Actinomycetes into carbonate substrates has not yet been investigated.

The heterotrophic or chemoautotrophic mode necessitated by endolithic life within buried sediments may explain the occurrence of these forms only in the molluscan shell fragments planted in the *Thalassia* zone. The lack of endoliths within inorganic calcite rhombs planted below the sediment-water interface may indicate parasitic or saprophytic requirements of these organisms. Boring might be an effort to obtain nutrients from the organic matrix of the molluscan substrates. No reasons are known for the lack of these endoliths in the deeper fore-reef sand-trough zone of Carrie Bow Cay. Although both this environment and the *Thalassia* zone consist of a carbonate sand bottom, the latter may contain more interstitial detrital organic matter or may be a more reducing environment. The availability of nutrients may control the distribution of these endoliths and therefore may explain the paucity of these forms within coarse sediments lacking necessary nutrient sources. Eh conditions within sediments may also be a controlling factor. Endolithic boring in this case may not be an "active" search for organic matrices in carbonate substrates, but a "passive" result of metabolic reaction or a form of protection from interstitial grazers.

FIGURE 70.—Scanning electron and transmitted light photomicrographs of unidentified microborings collected in subsurface station in the *Thalassia* zone: *a*, irregular polygonal network of varying intermittent borings, plastic cast within an etched mollusk fragment, 20 cm below the sediment-water interface; *b*, irregular polygonal endolithic network within molluscan substrate, collected 35 cm below the sediment-water interface; *c*, irregular, flattened aggregates associated with a polygonal network, these patches might be related reproductive bodies or separate colonial forms, plastic cast of acid-etched molluscan substrate; *d*, crenulate discoid associated with a polygonal network, this also might be a separate organism or related reproductive body, plastic cast of an etched mollusk fragment, 5 cm below the sediment-water interface. (Scale = 50  $\mu\text{m}$  for *a*, *c*, *d*; 25  $\mu\text{m}$  for *b*.)

**PALEOECOLOGIC AND GEOLOGIC SIGNIFICANCE.**—Endoliths and their borings found in carbonate sediments that are exposed on the sea floor may provide valuable information for the study of paleoecological conditions of carbonate sediments. The microborers and their distributional patterns at the sediment-water interface of Belize closely resemble those of assemblages previously examined in St. Croix, Jamaica, and Florida (Perkins and Tsentas, 1976). It thus becomes possible to identify endoliths typical of a tropical shallow marine setting and to establish their occurrence in upper photic and lower photic zones. Microborings commonly are preserved within ancient carbonates (Hessland, 1949; Gatrall and Golubic, 1970; Golubic et al., 1975), but they have not been examined in relation to recent zonations for the interpretation of paleoenvironmental conditions.

## Conclusions

Carbonate substrates, both conch shell fragments and cleaved calcite, planted just at the sediment-water interface in various depths along the reef transect off Carrie Bow Cay, Belize, contained a diverse assemblage of microboring forms. The blue-green alga *Hyella tenuior* and the green alga *Ostreobium brabantum* were restricted to the shallowest sample sites of the upper photic zone, which is also characterized by the abundant blue-green alga *Mastigocoleus testarum* and the green alga *Phaeophila engleri* and very little of the *Conchocelis*-stage of the red alga *Porphyra* sp. The lower photic zone, below approximately 12 m, is characterized by abundant *Porphyra* sp. and considerably less *M. testarum* and *P. engleri*. The blue-green alga *Plectonema terebrans* was abundant at all depths examined. Hyphae of fungal endoliths were present at all sample sites, although different sporangial forms were bathymetrically restricted. This study of algal endoliths supports previous findings of a distinct tropical assemblage that may provide a basis for paleoecological studies of ancient assemblages.

Below the sediment-water interface off Belize, endoliths infested only the molluscan (conch)

fragments in the *Thalassia*-zone station and were not present in material buried in a deeper fore-reef sand-trough station. Restriction of infestation to the molluscan shell fragments suggests that these subsurface endoliths require organic matrices as nutrient sources. Three types of endoliths occur below the sediment-water interface: (1) irregular filamentous networks, (2) irregular flat-

tened amorphous masses, and (3) regular crenulate discoids. These microborers have unknown taxonomic affinities but they closely resemble endolithic traces and scars attributed to fungi, bacteria, and Actinomycetes. Further studies are needed to explain the origin and geological importance of these possible environmental indicators and post-depositional carbonate degraders.

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# Production of Some Benthic Communities at Carrie Bow Cay, Belize

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## ABSTRACT

The primary production of *Thalassia testudinum*, mixed algae on coral rubble, and coral sand in the vicinity of Carrie Bow Cay, Belize, was estimated from in situ oxygen flux (by titrimetry) in enclosed chambers. *Thalassia* beds were autotrophic, yielding a daily net production in the range of 2.22–42.3 mg O<sub>2</sub> per square meter (approximately equivalent to 0.67–12.7 g C per square meter). The other habitats were heterotrophic despite considerable microalgal development, with a production/respiration ratio (P/R) less than unity. Contribution by the phytoplankton was negligible. Diurnal oxygen flux in open waters over *Thalassia* beds was typical for similar tropical areas.

## Introduction

In tropical coastal waters, coral reef ecosystems are generally considered to be highly productive in contrast to plankton communities, whose primary production is quite low or even negligible (Lewis, 1977; Milliman and Mahnken, 1969; Sournia, 1969). The metabolism of coral reefs as a unit has been the subject of numerous studies beginning with Sargent and Austin (1949) and Odum and Odum (1955). The remarkable fertility of reefs, their dynamic balance, and susceptibility to environmental perturbation have often been noted (see reviews by Lewis, 1977, and Johannes in Wood and Johannes, 1975).

The plants responsible for primary production in tropical coastal waters include mangroves, sea

grasses, macroscopic algae, boring and epipelagic algae, zooxanthellae, and phytoplankton. The relative importance of each group varies from area to area, but except for special environments such as enriched lagoons and upwelling areas (Sournia, 1969; Steeman-Nielsen, 1975), the contribution of phytoplankton is low. The techniques of investigating primary productivity have varied among investigators according to whether information is required on the productivity of the total community or its components, and according to the facilities and methods available. In general, chemical or polarographic measurements of oxygen flux are sufficiently precise for nonplanktonic biotopes, and these techniques have provided considerable information on the metabolism of tropical benthic communities (for instance, Lewis, 1977; McRoy and McMillan, 1977).

Reported here are results of production measurements in several habitats at and near Carrie Bow Cay, Belize. Topographic, oceanographic, and ecological characteristics of the area are presented elsewhere in this volume.

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## Methods

Oxygen flux was measured in three habitats: seagrass beds (*Thalassia testudinum* Banks ex König with small amounts of *Syringodium filiforme* Kützing) at depths of 1 to 3 m on the lagoon side of

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Carrie Bow Cay; mixed algal communities on coral rubble at depths of 0.5 to 1.0 m in the rubble and pavement zone behind the reef crest; and coral sand at a depth of 1 m in the back-reef zone. The coral rubble was composed of cobble-sized pieces of coral mixed with sand and with small (unidentified) filamentous, crustose, and thallose seaweeds. The coral sand first seemed devoid of organisms, but microscope examination revealed considerable numbers of blue-green algae, diatoms, Foraminifera with symbiotic algae, filamentous algae, and a multitude of other representatives of the micro- and meiobenthos.

Experiments were conducted over periods of dawn/noon, noon/sunset, and 24 h cycles with determinations at 1 or 2 h intervals, all during April/May 1977 and January 1978. For comparative purposes, the production of phytoplankton was also assessed.

For each experiment three transparent and two opaque polystyrene boxes of 500 cm<sup>2</sup> area were inverted over the substrate. The edges were pushed into the sediment to prevent leakage around the margin of the container. Water was withdrawn through sampling ports with a 50 ml capacity syringe. The total volume of enclosed water was 4.2 liters. For diurnal fluctuations in oxygen and phytoplankton production measurements, 300 ml biological oxygen demand (BOD) bottles were used.

Dissolved oxygen was measured titrimetrically by the Winkler method, using phenylarsine oxide (PAO) as titrant. PAO is superior to thiosulfate in its longer shelf life and resistance to bacterial decomposition, and produces results with comparable precision.

During the experiments water temperature varied from 26° to 29°C (by mercury immersion thermometer) and salinity varied from 34.4 to 35.2 ‰ (by Endeco refractometer type 102). As much as possible, all experiments were conducted on days that were cloud free, or nearly so.

## Results and Discussion

Results of a preliminary experiment to determine the diurnal variation in dissolved oxygen in

the open water over a *Thalassia* bed are shown in Figure 71. During predawn hours, characteristically, minimum oxygen concentrations are exhibited. The subsequent rapid increase of dissolved oxygen reflects photosynthetic activity (as light intensity increases). The daily oxygen maximum occurs at or somewhat after noon, at which time minute streams of oxygen bubbles frequently issue from some *Thalassia* blades. A gradual decline in oxygen concentration occurs during the rest of the day, becoming more pronounced in the late afternoon. Minimum concentration is again reached in the predawn hours. This pattern is typical and well documented, not only for tropical seagrass communities (for instance, Odum et al., 1959; Qasim and Bhattachari, 1971) but for coral reefs as well (for instance, Sournia, 1976a). For part of the day, the water is supersaturated, often in excess of 150%, with respect to oxygen. Some consequences of these conditions are discussed below.

Table 9 summarizes the production of the different communities. Oxygen data were converted to carbon assuming a photosynthetic quotient (PQ) of 1.25 (McRoy and McMillan, 1977; Westlake, 1963). The standing stock of *Thalassia* blades varied from about 34 to 126 g/m<sup>2</sup> dry weight, with a mean of about 47 g. Other organisms were not analyzed quantitatively.

Compared to published data for seagrass beds, summarized in Lewis (1977) and McRoy and

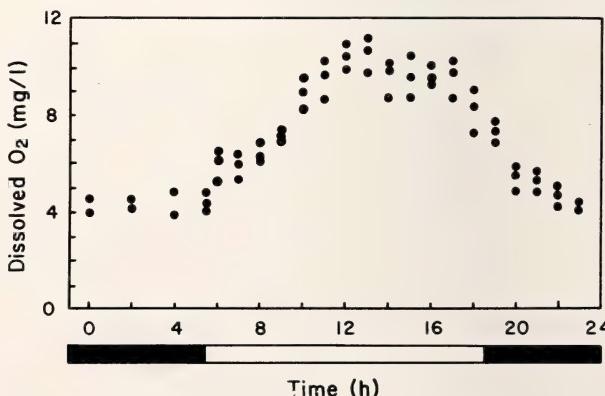


FIGURE 71.—Changes over a 24-hour period in dissolved oxygen over a *Thalassia* bed near Carrie Bow Cay, 28–29 April 1977.

TABLE 9.—Oxygen production of communities at Carrie Bow Cay, 26 April–5 May 1977, unless otherwise indicated (gross and net carbon production assumes  $PQ = 1.25$  (Westlake, 1963); phytoplankton assumes 1 m water depth)

Community	Trials (n)	Production (mg O <sub>2</sub> /m <sup>2</sup> /d)			P/R	Production (g C/m <sup>2</sup> /d)	
		Gross	Net	Respiration (mg O <sub>2</sub> /m <sup>2</sup> /d)		Gross	Net
<i>Thalassia</i> beds	5	19.3–118.1	6.03–42.30	13.27–75.80	1.45–1.56	5.79–35.43	1.81–12.69
<i>Thalassia</i> beds (Jan 1978)	3	14.9–33.2	2.22–14.50	12.68–18.70	1.18–1.78	4.47–9.96	0.67–4.35
Mixed algae/ coral rubble	3	60.0–94.3	-163.0–31.6	223.0–125.9	0.27–0.75	18.00–28.29	-48.90–9.48
Coral sand	2	75.5, 107.9	-11.3, -32.1	86.8, 140.0	0.87, 0.77	22.65, 32.37	-3.39, -9.63
Phytoplankton	2	0.48, 1.00	0.14, -0.07	0.34, 1.07	1.41, 0.93	0.14, 0.30	0.04, -0.02

McMillan (1977), the data for *Thalassia* at Carrie Bow Cay fall within previously noted ranges for gross and net production. The standing stock is rather low compared to several other localities in the Caribbean and Gulf of Mexico (refer to table 1 in McRoy and McMillan, 1977). In contrast to some *Thalassia* habitats in Puerto Rico (Odum et al., 1959), in the present case all measurements indicate a consistently autotrophic community, that is, ratio of production to respiration (P/R) in excess of 1. The wide range in measurements, in part attributable to density variations in *Thalassia* and seasonal differences, make extrapolations to an annual production uncertain. For comparative purposes the mean production for all *Thalassia* measurements may be estimated at 1800 g C/m<sup>2</sup>/y net production. This amount is higher than those reported from seagrass beds in Puerto Rico (Odum et al., 1959), but considerably less than those reported from Cuba and Florida (Buesa, 1972; Odum, 1957, 1963).

Differences in production were noted between late spring and winter. The extent to which these differences are significant is unknown because of the small number of replicates analyzed. Such variables as photoperiod (Marmelstein et al., 1968) and water temperature (citations in McRoy and McMillan, 1977) affect *Thalassia* production and add to the uncertainty of annual rate comparisons based on extrapolation.

A considerable area of the back-reef zone at Carrie Bow Cay consists of coral rubble and

pavement rock overgrown with a variety of small but conspicuous filamentous and thallose algae. Despite a gross production generally exceeding that of the *Thalassia* beds (Table 9), the community as a whole is heterotrophic, having a P/R less than 1. This habitat harbors a diverse and abundant fauna of burrowing invertebrates that contribute to the high community respiration. Grazing effects of fishes and large invertebrates, not considered here, are probably also significant in the consumption of primary producers (Marsh, 1976). The relative contribution of microalgal species in this habitat has generally been neglected, although Qasim et al. (1972) reported net production rates of 365–800 g C/m<sup>2</sup>/y for similar types of algae from the Laccadive Archipelago. Overall, the algal oxygen production in this habitat is less than oxygen consumption by herbivores and other animals.

Although the extensive coral sand areas north and northwest of Carrie Bow Cay appear to have few plant producers, microscopic examination revealed large numbers of benthic pennate diatoms and filamentous blue-green algae (or cyanobacteria), smaller numbers of Foraminifera with apparent endosymbiotic algae, and large numbers of micro- and meiobenthos metazoans. Community respiration slightly exceeded gross production, with P/R less than 1 (Table 9), although this habitat was closer to an autotrophic condition than the rubble-pavement habitat. The contribution of bacteria to community respiration

was not evaluated but it may be significant (see for instance, Edwards, 1978). The gross production approached that of the *Thalassia* beds, and therefore indicated the high photosynthetic activity here.

That such sand areas are not necessarily heterotrophic has been convincingly demonstrated by Sournia (1976b). Extensive development of the blue-green alga *Oscillatoria limosa* in sand at Moorea Island lagoon was responsible for an average gross production equivalent of over 6000 mg O<sub>2</sub>/m<sup>2</sup>/d with P/R = 1.5–3.0, a highly autotrophic habitat. Although blue-green algae are not abundant at Carrie Bow Cay, the potential contribution of coral sand areas should not be ignored in calculations of production in reef areas. Under some circumstances Foraminifera with endosymbiotic algae may dominate coral sands. Sournia (1976a) described sands from Takapota Atoll with a net production of 115–354 mg O<sub>2</sub>/m<sup>2</sup>/h (= 43–133 mg C/m<sup>2</sup>/h) and with populations consisting primarily of Foraminifera with endosymbionts. Small numbers of these protozoa were also present in sands at Carrie Bow Cay, but pennate diatoms dominated as primary producers.

These sands could potentially assume the autotrophic role that Sournia (1976a) described. A minor perturbation in the environment of organisms already under natural stress (by light and temperature thermal, among others) may shift community composition to one of low density consisting of eurytolerant species (Wood and Johannes, 1975). Several different species of blue-green algae, which certainly qualify as eurytolerant, can be observed in the sands of Carrie Bow Cay. Coral sand habitats have been largely neglected by ecologists, so that it would be useful to stress them experimentally in various ways in order to determine whether and how their trophic status is modified. Perturbation in the form of nutrient enrichment was attempted in one microatoll, resulting in significantly increased production (Kinsey and Domm, 1974).

As expected, the production of the phytoplankton was very low, and near the limits for accuracy

of the technique used (Table 9), supporting the conclusion that phytoplankton in the vicinity of coral reefs contribute a negligible amount to net production (Milliman and Mahnken, 1969; Sournia and Ricard, 1976). Although such shallow areas generally have, in addition to the normal complement of typically planktonic forms, a higher number of benthic diatoms swept into the water column by turbulence, net production remains negligible. For offshore Caribbean waters net production can be higher or lower than in reef areas, depending on locale. Beers et al. (1968) found 0.03–0.28 g C/m<sup>2</sup>/d offshore from Jamaica; Steeman-Nielsen and Jensen (1957) found 0.14 and 0.19 g C/m<sup>2</sup>/d in the south-central Caribbean Sea. In contrast, Ricard (1977) found higher production in the lagoon than in the open ocean at Tahiti, but the converse was true at Lakeba lagoon. Higher productivity is unquestionably possible under localized enriched conditions (Gordon et al., 1971; Margalef, 1975).

The limitations of technique and procedures used in this work deserve brief mention. Production in tropical benthic communities has been studied in several ways: by flow respirometry, which measures changes in the flux of carbon dioxide or oxygen (upstream-downstream); by in situ light/dark bottle methods using oxygen flux (titrimetric and polarographic) and various radioactive tracers; and by direct measurement of changes in standing stocks. All these methods are subject to errors and various assumptions (for discussion, see Lewis, 1977; Sournia, 1976c; Volkenweider, 1974) that will not be examined here, except to note that the technique used here appears to be satisfactory for benthic habitats. Unquestionably, accuracy decreases in the case of water supersaturated with oxygen; similarly, respiration of animals is affected by reduced oxygen levels. Recycling of oxygen in lacunae of *Thalassia* blades is another potential source of error (Hartmann and Brown, 1967).

The accuracy of conversion of oxygen flux to its equivalent carbon varies widely depending on the photosynthetic quotient assumed. This creates a problem in comparing the production rates

calculated by different authors. Photosynthetic quotients ranging from 0.86 to 3.00 are possible. This work follows Westlake (1963) in the assumption that  $PQ = 1.25$  is valid for natural tropical communities in favorable conditions.

Two important sources of tropical primary production have not been considered here, namely the coral zooxanthellae and the larger seaweeds. The complex role of the former in reef trophic structure has been discussed by Lewis (1977) and Marsh (1976) among others, and the contribution of zooxanthellae at Carrie Bow Cay is certainly worthy of investigation. Under some conditions the larger seaweeds contribute significantly to primary production, even more so than *Thalassia* beds (Doty, 1971; Wanders, 1976), but their development around Carrie Bow Cay is not extensive.

### Conclusions

Of the benthic habitats investigated at Carrie Bow Cay, *Thalassia* beds were most productive, yielding a maximum gross production of 35.4 g C/m<sup>2</sup>/d and a maximum net production of 12.7

g C/m<sup>2</sup>/d. Coral sand habitats and mixed algae with coral rubble habitats were heterotrophic in nature, despite considerable algal development. Net production by phytoplankton was negligible. The diurnal oxygen content of water flowing over *Thalassia* beds fluctuates in a manner typical of similar habitats previously described.

Given the problems inherent in comparing a wide variety of techniques and procedures, the pattern of primary production at Carrie Bow Cay is typical of similar tropical areas.

### Addendum

Since the writing of this contribution three pertinent papers have appeared. Two center on reef community metabolism elsewhere in the Caribbean (Puerto Rico, U.S. Virgin Islands) and also employ the Winkler method for oxygen determinations (Rogers, 1979; Rogers and Salesky, 1981). The third deals with primary production by microalgae in North Sea sediments comparing various techniques, including platinum electrode measurements that allow recording of dissolved oxygen microprofiles (Revsbech et al., 1981).

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# Macrobenthic Invertebrates in Bare Sand and Seagrass (*Thalassia testudinum*) at Carrie Bow Cay, Belize

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and Martha W. Young

## ABSTRACT

The generally accepted view that seagrasses support a more dense and diverse invertebrate fauna than sand areas devoid of such vegetation was tested in *Thalassia testudinum* beds of Carrie Bow Cay lagoon, Belize. Mechanisms regulating the distribution of invertebrates were also examined.

Core samples from five stations, ranging from bare sand to dense seagrass, indicated no clear-cut effect of seagrass versus bare sand on densities of polychaetes and mollusks. The numbers of species from all seagrass stations were not significantly higher than those from sand stations. Species diversities for all stations were influenced mainly by species richness, except for the station in dense seagrass where species evenness was high. The most abundant polychaete and mollusk species sampled were found at all stations.

The proportion of fine-grained sediments in the substrate increased progressively from bare sand into the seagrass. Encrusting coralline algae provide a major contribution to the fine sediments of the grass beds. Seagrass standing crop increased from the small seagrass patch to the dense *Thalassia* bed. Inorganic components made up 49% of live and 70% of dead seagrass.

This study found no relationship between seagrass standing crop and species densities of invertebrates. Intense predation pressure is proposed as the primary regulating mechanism of species

densities in the Carrie Bow lagoon. Experimental field studies are needed to clarify predator-prey interactions.

## Introduction

Seagrasses are widely thought to support a more dense and diverse invertebrate fauna than bare sediment devoid of such vegetation. Only recently has this generalization been subjected to rigorous quantitative sampling and experimental testing (Heck and Wetstone, 1977; Orth, 1977; Reise, 1977; Young and Young, 1978). The mechanisms of distribution examined by these workers primarily concern (1) food, (2) living space, (3) predation, and (4) sediment stability.

**FOOD.**—Because seagrasses decompose rapidly relative to other vascular plants in the marine environment, they are considered to be major contributors to the detrital food web of seagrass ecosystems (Fenchel, 1977). Heck and Wetstone (1977) suggested from their work in Panama that food reserves are abundant in seagrass ecosystems and that food is not a limiting factor. Young and Young (1978), however, have experimentally demonstrated that numbers of certain deposit-feeding invertebrates are food-limited in a seagrass detritus-rich habitat in Florida and that significant increases in overall macrobenthic densities result from addition of detrital food with high nitrogen content.

**LIVING SPACE.**—Increased surface area afforded

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by topographically complex living and nonliving substrata has been defined as an important ecological parameter on the study transect at Carrie Bow Cay (Dahl, 1973; Rützler and Macintyre, herein: 9). Dahl (1973) has estimated that the functional surface area of bare sand is increased over four times by the presence of seagrass in the Carrie Bow Cay lagoon. Young and Young (1978) have experimentally shown no significant decreases in overall species densities of macrobenthos following the clipping and removal of seagrass blades from an area in a Florida seagrass bed, although the abundance of several seagrass-associated species diminished.

**PREDATION.**—Heck and Wetstone (1977) suggested that plant blades provide protection to epifauna from visually searching fish predators. Orth (1977) and Reise (1977) provided experimental evidence that seagrass roots and rhizomes decrease the effectiveness of crab predators upon infauna. Reise (1977) has also shown that coarse-grained sediments afford protection to infauna from crab predation more than fine-grained sediments. Because finer sediments accumulate more in seagrass beds relative to adjacent areas bare of vegetation (Orth, 1977), a clear-cut assessment of the effect of sediment size versus that of seagrass upon intensity of predation cannot be discerned in most seagrass areas.

**SEDIMENT STABILITY.**—Seagrass roots and rhizomes bind loose sediments together, and their blades baffle waves; both actions assist in preventing sediment resuspension and erosion (Ginsburg and Lowenstam, 1958). Orth (1977) has demonstrated that the overall sediment stabilizing effect of seagrasses is a major factor in increased densities and diversity of infauna of seagrass beds in Chesapeake Bay and Bermuda.

Our primary intent in this study was to determine whether densities of macrobenthic invertebrates in the Carrie Bow Cay lagoon were related to the presence of vegetation and, within the time constraints, which mechanisms were regulating the distribution of species.

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### Study Area and Methods

The lagoon floor of Carrie Bow Cay is covered by calcareous sediment comprised largely of coral, encrusting coralline algae, *Halimeda*, molluscan, foraminiferal, and echinoid material. The sand surface in areas lacking vascular vegetation is here and there covered with a fine filamentous algal "felt" (Dahl, 1973). The seagrass *Thalassia testudinum* Banks ex König grows profusely in these sediments, and grades from small, thinly vegetated patches (from the back-reef region) to the extensive, dense beds of the lagoon. The *Thalassia* is interspersed with sparse stands of the seagrass *Syringodium filiforme* Kützing. *Thalassia* blades are heavily encrusted with coralline algae and conspicuously devoid of epizoans, with the exception of Foraminifera.

We extended the established transect (Rützler and Macintyre, herein) from its beginning point at the buoy (0 m) lagoonwards 5 m into a dense bed of *Thalassia* (Figure 72). Station 1 (+23 m) was an area of bare sand containing no vegetation, station 2 (+18 m) was a small patch of *Thalassia*, station 3 (+12 m) was in bare sand, station 4 (+5 m) was in *Thalassia* at the edge of an area densely covered with seagrass, and station 5 (-5 m) was inside the *Thalassia* bed. Because of the depth of water at the sampling locations (approximately 2 m) and the small tidal variation (0.2 m tidal range, Kjerfve, 1978), seagrasses in this area of the lagoon are never exposed at low tide. Salinity was 34‰ throughout the sampling period and water temperature varied from 27° to 28° C. The grass area sampled at station 2 is approximately 80 m from the nearest patch reefs. The sand areas (stations 1 and 3) are at the same depth as adjacent seagrass stations. These bare

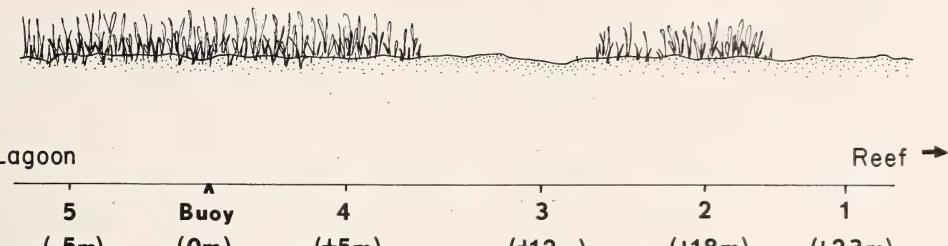


FIGURE 72.—Diagrammatic representation of the transect in Carrie Bow Cay lagoon showing sampling stations for this study; the buoy marks the beginning of the main transect (Rützler and Macintyre, herein), which was extended, for purposes of this study, 5 m into dense *Thalassia* (distance from zero point in parentheses).

sand stations show no traces of scour or ripple marks.

Samples were taken from 23 to 31 March 1976 with a PVC corer (9.45 cm in diameter) to a depth of 20 cm ( $= 1405 \text{ cm}^3$ ) at five stations along a 28 m long transect. Each sample consisted of four replicate cores taken perpendicular to the transect at each sampling station. The number of replicate cores per sample was determined by analyses of pilot samples taken in dense *Thalassia* from the lagoon. Four replicate cores contained 90% or more of the species of polychaetes and mollusks expected according to the test of Gaufin et al. (1956). Samples taken in *Thalassia* included blades, roots, and rhizomes.

Samples were sieved through 1.0 mm mesh Nytex screen, narcotized with 0.15% propylene phenoxytol in sea water, stained with rose bengal and fixed in 5% to 10% formalin in sea water. Organisms were transferred to 70% ethyl alcohol after 24 hours for sorting, identification and storage. In this study, the term "macrobenthos" refers to those benthic invertebrates retained on a 1.0 mm mesh screen. Sampling efficiency of 1.0 mm mesh was determined by screening one of the replicates from each station through both 0.5 mm and 1.0 mm mesh screen. Only whole animals, anterior fragments of polychaetes and live shells of mollusks were identified as to species and counted. All other macrobenthos were identified only to higher taxonomic categories and counted.

One sediment sample (comprising four replicate cores) was taken with the PVC corer at each

station. Particle sieve size was determined using a Ro-Tap and analyzed by the method of Folk (1974). Samples from each particle size category were examined microscopically.

All seagrass blades were clipped at the sediment surface and shoots were counted from one-meter-square areas adjacent to stations 2, 4, and 5. Erect live seagrass blades and prostrate dead blades were collected separately from each clipped plot. Live and dead seagrass dried at 100° C for 48 hours and weighed provided an estimate of seagrass standing crop at each station. Organic and inorganic composition was determined from the ash of both live and dead fractions processed at 550° C for 2 hours.

A random sample of *Thalassia* blades that showed evidence of grazing by herbivorous fishes was collected, and bite marks were counted and measured.

Data were analyzed ( $\log_2$ ) using Shannon's information measure of species diversity,  $H'$  (Pielou, 1966); species richness,  $d$ , was determined by the method of Margalef (1958), and species evenness by  $E'$  (Buzas and Gibson, 1969). A one-way analysis of variance (ANOVA) using non-transformed data compared numbers of species as well as species densities at the 5 stations. The a posteriori Student-Newmans-Keuls (SNK) multiple comparison test was run, since in both cases the ANOVA indicated significant differences among means (Sokal and Rohlf, 1969). Significance for the ANOVA and SNK tests was chosen at the 95% level of confidence.

TABLE 10.—Taxa and number of specimens of 60 polychaetes and 23 mollusks from five stations in the Carrie Bow Cay lagoon (sp. = unidentified species; sp. A = presumed new species)

Taxon	Station					Taxon	Station					Total no. of specimens	Total no. of specimens	
	1	2	3	4	5		1	2	3	4	5	Rank		
POLYCHAETA														
<i>Clymenella mucosa</i> (Andrews)	41	10	15	18	7	1	91							
<i>Jasminea</i> sp.	31	10	44	4	1	2	90	Sars	0	4	3	2	3	18
<i>Parionosyllis longicirrata</i> (Webster and Benedict)	12	13	26	17	11	3	79	<i>Lambineris latrelli</i> (Audouin and Milne-Edwards)	0	0	6	6	0	18
<i>Sphaerosyllis pinnifera</i>	26	10	30	0	4	4	70	<i>Prionospio heterobranchia</i> Moore	0	2	5	2	3	18
Claparède								<i>Laeonereis culveri</i> (Webster)	2	2	5	0	0	19
<i>Exogone dispar</i> (Webster)	2	7	16	22	5	5	52	<i>Trichobranchus glacialis</i> Malmgren	5	0	0	4	0	19
<i>Syllis</i> ( <i>Typosyllis</i> ) <i>hyalina</i> Grnbe	0	27	1	9	9	6	46	<i>Lambrinurus tetrura</i> (Schmarda)	4	4	0	0	0	9
<i>Protodorvillea kefersteini</i>	4	7	17	2	5	7	35	<i>Chaetopteridae</i> sp. A <i>Nichomache antillensis</i> Augener	0	3	0	4	1	20
McIntosh	2	3	12	7	9	8	33	<i>Thelodus setosus</i> (Quatrefages)	0	0	7	0	1	20
<i>Omphis microcephala</i>								<i>Proceraea</i> sp.	7	0	0	0	0	8
Hartman	5	5	5	9	5	9	29	<i>Magelona petiboneae</i>	1	1	3	1	1	7
<i>Syllis</i> ( <i>Langerhania</i> ) <i>cornuta</i>	0	5	0	5	18	10	28	Jones	7	0	0	0	0	7
Rathke								<i>Terebellidae</i> juv. <i>Magelona nojai</i>	0	0	0	6	0	7
<i>Plathynereis dumetili</i> (Audouin and Milne-Edwards)	3	8	2	5	3	11	21	Jones	1	4	0	1	0	6
<i>Glycera abranchiata</i>								<i>Caulernella</i> sp.	0	3	0	3	0	6
Treadwell	0	1	5	9	5	12	20	<i>Chone daneri</i>	0	1	3	1	0	6
<i>Anisostyllis rigida</i>								<i>Cratonereis mirabilis</i>	2	2	1	0	0	5
Fauvel	2	3	10	2	0	13	17	Kinberg	0	3	0	2	0	5
<i>Euryyllis tuberculata</i>								<i>Nereidae</i> juv. <i>Phyllodoce</i> ( <i>Anaitides</i> ) <i>panamensis</i>	0	4	0	0	0	4
Ehlers	0	0	7	8	1	14	16	Treadwell	0	0	0	2	2	4
<i>Euryllis blomstrandii</i>								<i>Spinorbis</i> ( <i>Janua</i> ) <i>cornutus</i>	0	0	0	2	2	4
Malmgren	0	8	3	1	4	14	15	<i>Montagu</i>	0	1	1	1	0	3
<i>Mediomastus ambiseta</i> (Hartman)	4	6	3	1	0	16	14	<i>Eunynthia</i> <i>chilensis</i>	0	0	0	0	0	3
<i>Capitella capitata</i> (Fabricius)								Kinberg	0	0	0	0	0	2
<i>Aedictira belgicae</i> (Fauvel)	6	5	1	1	0	17	13	<i>Naineris laevigata</i>	0	0	0	3	3	3
<i>Pholoe minuta</i> (Fabricius)	1	7	1	1	3	17	13	Fauvel	2	0	0	0	0	2
<i>Polyvirrus</i> sp.	6	1	0	5	0	18	12	<i>Bhawania godei</i>	2	0	0	0	0	2
<i>Lysidice ninetta</i>								Webster						

TABLE 10.—Continued

Taxon	Station					Taxon	Station					
	1	2	3	4	5		1	2	3	4	5	Rank of specimens
<i>Sabellidae</i> juv.	2	0	0	0	0	26	2	<i>Solemya occidentalis</i>	0	2	2	3
<i>Eunice sicilensis</i>	0	1	0	1	0	26	2	Deshayes	0	5	0	4
<i>Grube</i>								<i>Phyllaphysa engeli</i>	0	5	0	10
<i>Podarke obscura</i>	0	2	0	0	0	26	2	Marcus	0	1	0	7
Verrill								<i>Acmaea pustulata</i>	0	1	0	5
<i>Cirratulus</i> sp.	0	1	1	0	0	26	2	(Helbling)	0	3	1	7
<i>Hesionura elongata</i>	0	0	1	1	0	26	2	<i>Actaecia canadensis</i>	1	1	0	5
(Southern)								(Orbigny)	1	1	1	4
<i>Branchiomma nigromaculata</i>	0	0	0	0	2	26	2	<i>Americardia gryphi</i>	1	1	0	7
(Baird)								Thiele	2	0	0	3
<i>Lepidionotus</i> sp.	1	0	0	0	0	27	1	<i>Lucina pectinata</i>	2	0	0	8
<i>Eutalia viridis</i>	0	1	0	0	0	27	1	(Gmelin)	1	0	1	3
(Linnaeus)								Bivalve juv.	0	1	0	3
<i>Sigalion arenicola</i>	0	1	0	0	0	27	1	<i>Dentalium antillarum</i>	0	1	1	3
Verrill								Orbigny	0	0	1	2
<i>Bhavania</i> sp. A	0	1	0	0	0	27	1	<i>Tellina versicolor</i>	0	0	1	3
<i>Spionidae</i> sp.	0	0	1	0	0	27	1	DeKay	1	0	1	2
<i>Arabella bicolor</i>	0	0	1	0	0	27	1	<i>Olivella nivea</i>	1	0	1	3
(Montagu)								(Gmelin)	1	1	0	2
<i>Capitella jonesii</i>	0	0	1	0	0	27	1	<i>Ithythyara parkeri</i>	1	1	0	2
(Hartman)								Abbott	0	1	0	9
<i>Pista cristata</i>	0	0	1	0	0	27	1	<i>Smaragdia viridis</i>	0	1	0	2
(Muller)								(Linnaeus)	0	0	1	2
<i>Polydora tigris</i>	0	0	0	1	0	27	1	<i>Polinices lacteus</i>	0	0	1	2
Webster								(Guilding)	1	0	0	9
<i>Tharyx marioni</i>	0	0	0	0	1	27	1	<i>Marginella ebenaola</i>	1	0	0	1
(Saint-Joseph)								Conrad	1	0	1	1
<i>Spinachaeopterus costarum oculatus</i>	0	0	0	0	1	27	1	<i>Abra aequalis</i>	1	0	0	1
Webster								(Say)	0	1	0	1
<i>Harmothoe aculeata</i>	0	0	0	0	1	27	1	Turridae sp.	0	1	0	1
Andrews								<i>Codakia orbicularis</i>	0	1	0	1
								(Linnaeus)	0	0	0	1
								<i>Tellina probina</i>	0	0	0	1
								Boss	—	—	—	—
								<i>Pitar</i> sp. A.	0	0	1	1
								<i>Cadulus quadridentatus</i>	0	0	1	1
								(Dall)	0	1	0	1
								<i>Divericella quadrivalvis</i>	0	0	1	1
								(Orbigny)	—	—	—	—
								Total	882	—	—	—
								Total	—	—	—	—
								MOLLUSCA	—	—	—	—
								<i>Bulla striata</i>	—	—	—	—
								<i>Bruguirea</i>	—	—	—	—
								<i>Chione cancellata</i>	—	—	—	—

## Results

Polychaetes and mollusks represented 51% of 1960 individuals collected in 20 core samples. Nematodes, oligochaetes, and arthropods comprised 47% and miscellaneous other groups (predominantly sipunculids, anthozoans, and echinoderms) comprised 2% of the total macrobenthos. Numerical dominance and the fact that our species identifications were most complete for polychaetes and mollusks led us to assume that these taxonomic groups adequately represent the macrobenthos at the community level of organization. A comparison of rankings of polychaetes and mollusks from all five stations (Table 10), using a grand mean of two specimens per species per station as a criterion, shows that nine species were common to both bare sand and areas con-

taining *Thalassia*; only three species (*Platynereis dumerilii* (Audouin and Milne-Edwards), *Capitella capitata* (Fabricius), and *Phyllaplysia engeli* Marcus) were found in seagrass alone. Mean densities (extrapolated) of 8000/m<sup>2</sup> (polychaetes and mollusks) were sampled in bare sand and 6476/m<sup>2</sup> (polychaetes and mollusks) in *Thalassia*.

The faunal list given in Table 10 is not intended to be all inclusive. Several species found among grass blades from the clipped meter square areas did not appear in the core samples, for example, the mollusks *Astrea phoebia* Röding, *Tricolia thalassicola* Robertson, and *Alaba incerta* (Orbigny).

Figure 73 shows numbers of individuals and species of polychaetes and mollusks per sample at each of the five stations. The number of individuals at station 3 was significantly (SNK) different

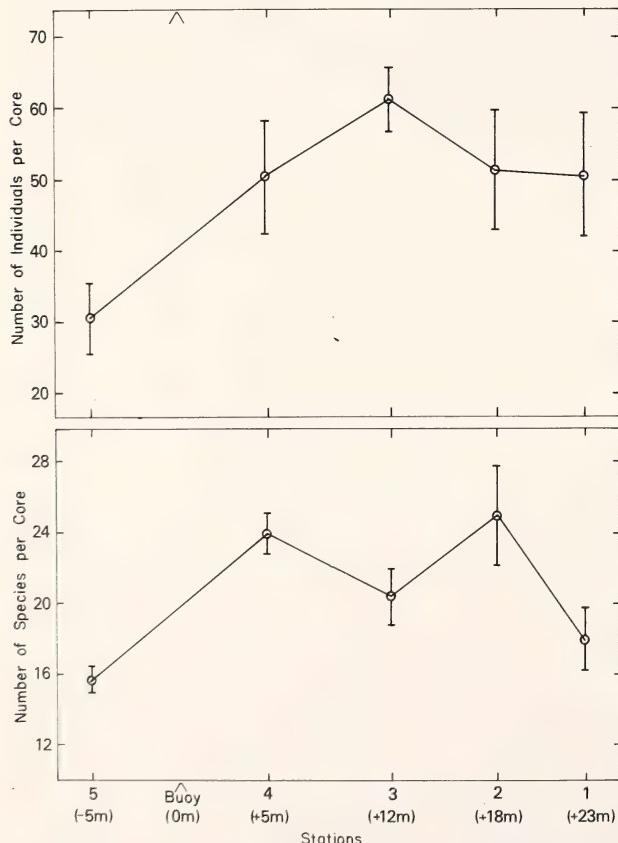


FIGURE 73.—Numbers of individuals and numbers of species of polychaetes and mollusks per core ( $\bar{x} + S\bar{x}$ ) at five stations in the Carrie Bow Cay lagoon.

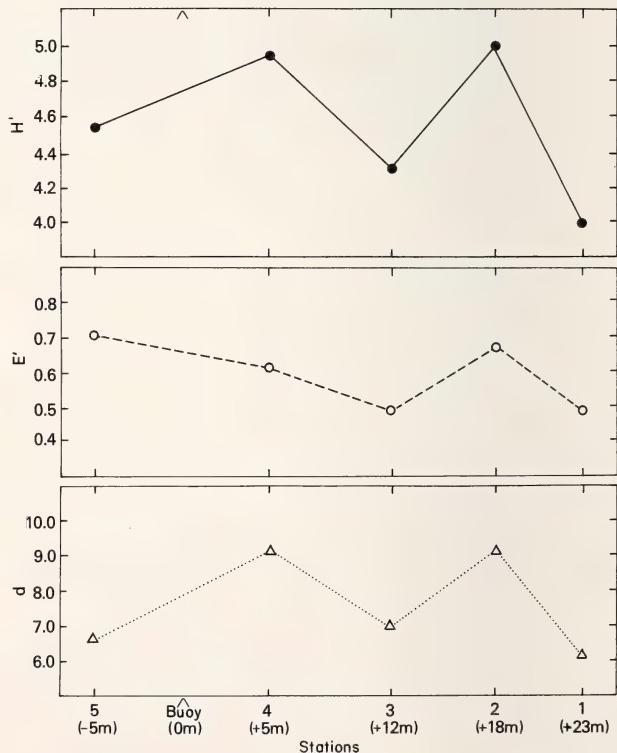


FIGURE 74.—Species diversity ( $H'$  with solid lines and solid circles), species evenness ( $E'$  with dashed lines and open circles), and species richness ( $d$  with dotted lines and open triangles) of polychaetes and mollusks at five stations in the Carrie Bow Cay lagoon; each sample consists of four replicate cores.

TABLE 11.—Standing crop of *Thalassia* per square meter at three stations in the Carrie Bow Cay lagoon; dry weights and percentages of organic and inorganic (after ashing) fractions compared for live and dead blades

Station	No. of shoots	Total dry weight (g)	Live blades			Dead blades		
			Wt. (g)	Org. (%)	Inorg. (%)	Wt. (g)	Org. (%)	Inorg. (%)
2	117	104.04	58.73	51	49	45.31	27	73
4	136	79.59	57.49	51	49	22.10	34	66
5	422	338.07	178.67	52	48	159.40	31	69

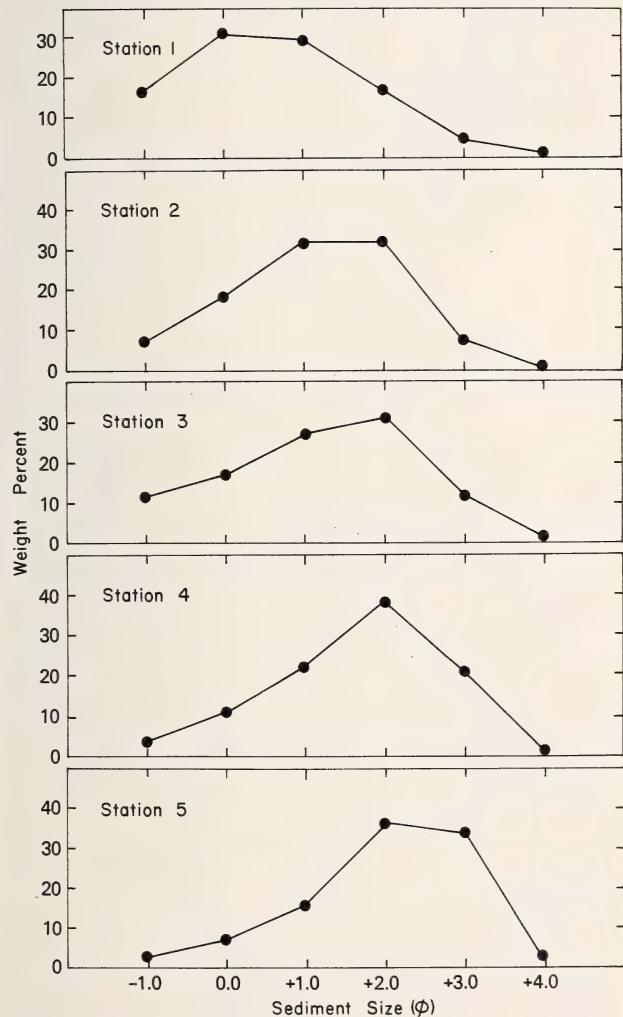


FIGURE 75.—Sediment size analyses at five stations in Carrie Bow Cay lagoon. Weight percentages of sediment sizes ( $-1.0$  to  $+4.0 \phi$ ) at each station.

(95% level of confidence) from that at station 5. All other stations, whether containing *Thalassia* or no vegetation, were not significantly different from one another. When numbers of species at all

stations were compared, stations 2 and 4 were significantly (SNK) different (95% level of confidence) from stations 1 and 5. Station 3 was not significantly (SNK) different from all other stations.

Figure 74 shows that species diversity and richness indices for all stations except station 5 reflect the same trend shown by numbers of species. The higher species diversity at station 5 (dense *Thalassia*) compared to stations 1 and 3 (bare sand) was largely due to the effect of high species evenness at station 5. Species evenness was higher in all seagrass stations than in bare sand stations.

Grass blades included in core samples contained eight polychaetes that had burrowed into the tissue of the grass blade, in some cases leaving a trail of fecal pellets behind them. These represent a variety of families: three capitellids, three syllids, one maldanid, and one sabellid. This phenomenon is not explained.

Although 216 additional specimens of polychaetes and mollusks were added by the 0.5 mm mesh from five cores (one from each station), only one species (the mollusk, *Caecum ryssotitum* Folin) was found that did not occur in 1.0 mm mesh samples.

Gravimetric measurements (Table 11) of both live and dead blades of *Thalassia* clipped from one meter square areas adjacent to stations 2, 4, and 5 show that seagrass standing crop increased from the patch at station 2 to the dense growth at station 5. Overall, 49% of living plant material and 70% of dead grass were inorganic in composition, whereas 51% and 30% respectively were organic.

Sediment size analyses (Figure 75) indicated that the percentage of fine sand (2 and 3  $\phi$ )

relative to coarse sand ( $-1$  and  $0 \phi$ ) increases from station 1 to station 5.

An examination of 20 randomly selected *Thalassia* blades with bite marks revealed  $5.5 \pm 0.9$  ( $\bar{x} + Sx$ ) bites per blade, with a diameter of  $7.8 \pm 0.3$  mm ( $\bar{x} + Sx$ ).

## Discussion

Although extrapolated densities of macrobenthos per meter square in the Carrie Bow Cay habitat (total fauna:  $12,167/m^2$  in *Thalassia*;  $16,750/m^2$  in bare sand) fall within the ranges reported for subtropical and tropical locations (Table 12), this study does not show a direct relationship among seagrass standing crop, species densities, and numbers of species. Although some invertebrates may benefit from the protection and living space afforded by blades, roots, and rhizomes, the overall composition of seagrass and bare sand assemblages of macrobenthos indicates that there is no clear-cut effect of seagrass versus bare sand on species densities. In fact, species densities are significantly (SNK) higher at one of the bare sand stations (station 3) than at the dense seagrass station (station 5). Numbers of species from seagrass stations differ significantly (SNK) from those collected in bare sand stations, with the exception of station 5. Numbers of species at station 5, in dense *Thalassia*, do not significantly differ from those in bare sand stations (stations 1 and 3).

The abundant species of polychaetes and mollusks are found in both sand and seagrass. Among the polychaetes, seven of the ten top ranked species are common to all stations. Only three species, the polychaetes *Platynereis dumerili* and *Capitella capitata* and the opisthobranch *Phyllaplysia engeli*, have relatively high densities in seagrass and not in bare sand. In this habitat, all three species live closely associated with seagrass blades: *P. dumerili* builds tubes on the blades, *C. capitata* tunnels within the tissue of the blades, and *P. engeli* feeds upon seagrass epiphytes.

In other studies comparing animal assemblages of sand and seagrass, the water depths, tidal

range, hydrography, and sediment characteristics have differed from those considered here. For example, along the sampling transect at Carrie Bow Cay the sediment interface between *Thalassia* beds and adjacent bare sand is imperceptible and not evidenced by erosional ridges (Jackson, 1972) or sand bars (Orth, 1977). Nor is there any indication in the study area of erosion around the rhizomes of seagrass plants or exposure of the root system, in a pattern of "raised terraces" (Kikuchi and Pérès, 1977). In other words, the transition from sand to seagrass off Carrie Bow Cay is marked only by the advent of vegetation and by a gradual lagoonward decrease in sediment grain size. There is no evidence of sedimentary bedload movement in the form of ripple marks (Santos and Simon, 1974). Because the bare sand areas studied are physically stable, no effect of sediment instability on densities or species composition of macrobenthos is evident.

The overall small size of specimens indicates that few macrobenthic invertebrates survive to maturity in this habitat. Only a few specimens fall within the mature size ranges reported in the literature; the lack of such larger sizes off Carrie Bow Cay implies high and persistent predation. The *Thalassia* and adjacent bare sand environments here may be defined, according to the model of Connell (1975), as having benign physical conditions in which predators usually kill all young colonists each year, and thereby reduce competition for resources (for instance, food and space) and help to perpetuate a state of nearly continual recolonization. Connell's model accounts for an occasional event in time and space wherein certain prey species can reach invulnerable sizes.

While seasonality may be less influential in a tropical than a temperate habitat, seasonal differences in densities of macrobenthos clearly should be expected in the habitat studied here. Nevertheless, our expectation that macrobenthic densities would correlate positively at any given time with seagrass was not substantiated by the evidence from this study.

In Carrie Bow lagoon, a majority of *Thalassia*

TABLE 12.—Published data on densities of macrobenthic invertebrates per square meter in seagrass and bare sand from subtropical and tropical benthic studies

Reference	Substrate		Sieve mesh size (mm)	Location
	Seagrass	Bare sand		
Bloom et al., 1972	—	510	1.0	Tampa Bay, Florida
Virnstein, 1972	—	17,151	0.5	Tampa Bay, Florida
Santos and Simon, 1974	33,485 <sup>a</sup>	8795 <sup>a</sup>	0.5	Tampa Bay, Florida
Young et al., 1976	3994–14,236	—	1.0	Indian River, Florida
McNulty, 1970	—	291 (1956) 108 (1960)	1.0	Biscayne Bay, Florida
Brook, 1975	4000 (1972) 1895 (1973)	—	1.0	Card Sound, Florida
Brook, 1978	292–10,644 4508	—	1.0	Biscayne Bay, Florida Florida Bay, Florida
Murina et al., 1973	583	354	1.0	Cuba
Young and Young, this study	12,167 6476 <sup>b</sup>	16,750 8000 <sup>b</sup>	1.0	Carrie Bow Cay lagoon, Belize

<sup>a</sup> Polychaetes only.

<sup>b</sup> Polychaetes and mollusks only.

blades were thickly encrusted with epiphytic coralline algae at the time of sampling. Humm (1964) notes that such encrusted blades sink to the bottom when they are broken off the parent plant and are not readily carried to other areas by tidal currents as are nonencrusted blades. In addition, observations of seagrass along the transect of this study suggest that individual *Thalassia* blades are increasingly weighted down by heavy growths of encrusting coralline algae at their tips, so that dead blades are commonly retained in situ. Gravimetric measurements of live and dead seagrass clipped from meter-square plots at stations 2, 4, and 5 show that 49% of the total biomass of live grass and 70% of dead seagrass consisted of inorganic material. Microscopic examination of this inorganic residue revealed mainly fragments of coralline algae. It is likely that coralline algal epiphytes on *Thalassia* contribute substantial carbonate sediments to the lagoon at Carrie Bow in a manner similar to that reported in Florida (Humm, 1964) and in Jamaica (Land, 1970). Patriquin (1972) estimated that the annual carbonate production by encrusting coralline algal epiphytes on *Thalassia* in Barbados is 2800 g/m<sup>2</sup>.

Grazing fish help to distribute a portion of the epiphytic crust on seagrass blades—sometimes widely beyond the seagrass beds (Randall, 1967). Numerous reef fishes, in mixed schools (mainly scarids and acanthurids), were observed moving between the patch reefs of the back reef area and the seagrass of the lagoon. Although schools of fish were observed among the seagrasses, individual fish appeared to feed on seagrass blades and the sediment between. Direct feeding on seagrass is evident from many bite marks on the edges of the blades. Thomas et al. (1961) reported similar crescent-shaped bites on *Thalassia* blades, and Zieman (1974) attributed these bite marks to the scarid, *Sparisoma radians*. Conspicuous bands of bare sand between reef areas and adjacent seagrass beds in the Virgin Islands have been related by Randall (1965) to heavy grazing by parrot fish (scarids) and surgeon fish (acanthurids). Primary invertebrate grazers of seagrass, such as echinoids (Margalef and Rivero, 1958), were not observed in the Carrie Bow lagoon.

Until night observations are made, we cannot determine whether invertebrate-feeding fishes such as pomadasysids (grunts) migrate nocturnally from the reefs to the seagrasses of the lagoon, as

described in the West Indies by Kikuchi and Pérès (1977). Decapod crustacean predation on other members of the macrobenthos may be important as a regulator of species densities, as suggested by Young et al. (1976) in Florida seagrasses. Caging experiments in both seagrass and bare sand areas, as in the Indian River lagoon, Florida, by Virnstein (1978), would help to determine the relative impact of fish and decapod predation in the Carrie Bow lagoon.

This study provides only indirect evidence to suggest that "within-community" predation may be intense among the macrobenthic species of Carrie Bow. Large numbers of bored shells of bivalves and gastropods were found in our samples; in all cases, numbers of bored shells greatly exceeded numbers of live shells. The only drill species was *Polinices lacteus* (Guilding), a naticid reportedly responsible for heavy predation on a wide variety of mollusks in *Thalassia* beds in Jamaica (Jackson, 1972). Polychaetes of the family Syllidae were extremely abundant in samples from both bare sand and *Thalassia* of Carrie Bow lagoon; five species of syllids are ranked among the 10 most abundant macrobenthic species. Murina et al. (1973) also reported large numbers of syllids in Cuban seagrass beds. Syllids are believed to be carnivorous (Pettibone, 1963; Day, 1967), preying on other invertebrates. As often is the case, ecological information is lacking for most of the species collected here, so that details of predator-prey interactions among the macrobenthos remain largely speculative.

## Conclusions

The data from this study do not substantiate the generalization that seagrasses support a more diverse and dense invertebrate fauna than areas without seagrasses. There are no significant differences in species densities of macrobenthos between seagrass and bare sand off Carrie Bow Cay. Significant differences do not exist among numbers of species of polychaetes and mollusks from all seagrass stations and from bare sand stations.

We suggest that the primary mechanism responsible for the regulation of macrobenthic species densities and diversities in the Carrie Bow lagoon is high and persistent predation. Intense predation pressure probably limits the presumed advantages of the more variable habitats and increased living space provided by seagrasses. Predator-prey interactions could be clarified by the use of field-experimental techniques such as caging.

Sediment instability appears to be unimportant in the regulation of macrobenthic species densities and diversities in the lagoon.

Few macrobenthic species are associated exclusively with seagrasses off Carrie Bow Cay. The majority of species sampled are common to both bare sand and seagrass stations.

Sediment size analyses showed a progressive increase of fine-grained sediments from bare sand into seagrasses. Important contributors to these fine sediments are coralline algal epiphytes on *Thalassia*.

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# A Submarine Cave near Columbus Cay, Belize: A Bizarre Cryptic Habitat

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## ABSTRACT

An unusual cryptic habitat having an extensive covering of serpulid worms has been discovered in a submerged Pleistocene cave in the Belize barrier-reef platform near Columbus Cay. Aggregates of serpulids, which have been named "pseudostalactites," project from the ceiling of this cave in the direction of a narrow opening (10 m long and less than 3 m wide) that breaches the roof of the cave at a water depth of 17 m. Apparently this opening has restricted the movement of water within the cave so that serpulid worms have become more abundant on the ceiling than other cryptobiota, which include some sponges, filamentous algae, mollusks, and bryozoans. The latter group, with the exception of boring bivalves, occurs only within a radius of 25 m from the entrance of the cave. The pseudostalactites are composed mainly of serpulids belonging to two species of the *Vermiliopsis glandigera infundibulum* group and extend at least 40 m from the cave opening, which is the limit of our observations. Varying amounts of submarine cement consisting of magnesium calcite form a coating on, or matrix in, the serpulid aggregations. A barren sediment cone (very fine sand to mud) occurs at a depth of 30 m below the cave opening.

## Introduction

In 1977 a Belizean SCUBA diver sent us a "stalactite" sample approximately 15 cm long

and 5 cm in diameter that he had collected from a submarine cave near Columbus Cay. This fragment had two surprisingly different sides: one composed predominantly of serpulid tubes and the other composed of dense microcrystalline Mg calcite forming a knobby surface. In our subsequent search for the source of this sample, we discovered an unusual megacryptic environment. This paper presents the results of our preliminary investigation of the biological and geological characteristics of a highly unusual habitat.

**ACKNOWLEDGMENTS.**—We are grateful to H. Bowman, Jr., and A. Usher of Dangriga for bringing this submarine cave to our attention. We thank K. E. Bucher, W. Gerwick, G. L. Hendler, P. M. Kier, W. M. Kier, R. J. Larson, K. Muzik, A. B. Rath, and P. E. Videtich for their field assistance. G. L. Hendler, W. M. Kier, and A. B. Rath also took underwater photographs. For help with identifications we thank A. H. Cheetham (bryozoans), I. M. Goodbody (tunicates), and R. S. Houbrick and T. R. Waller (mollusks). R. B. Burke provided the aerial photograph of the cave site and V. Krantz provided other photographic assistance. I. Jewett drafted the diagrams.

## Description of the Submarine Cave

**AEREAL SETTING.**—The submarine cave about 1 km northwest of Columbus Cay ( $17^{\circ}00'N$ ,  $88^{\circ}02'W$ ) occurs in a *Thalassia*-covered lagoon (5 m deep) at a distance of about 3 km inside the outer edge of the Belizean barrier reef platform (Figure 76). The only other natural depression in

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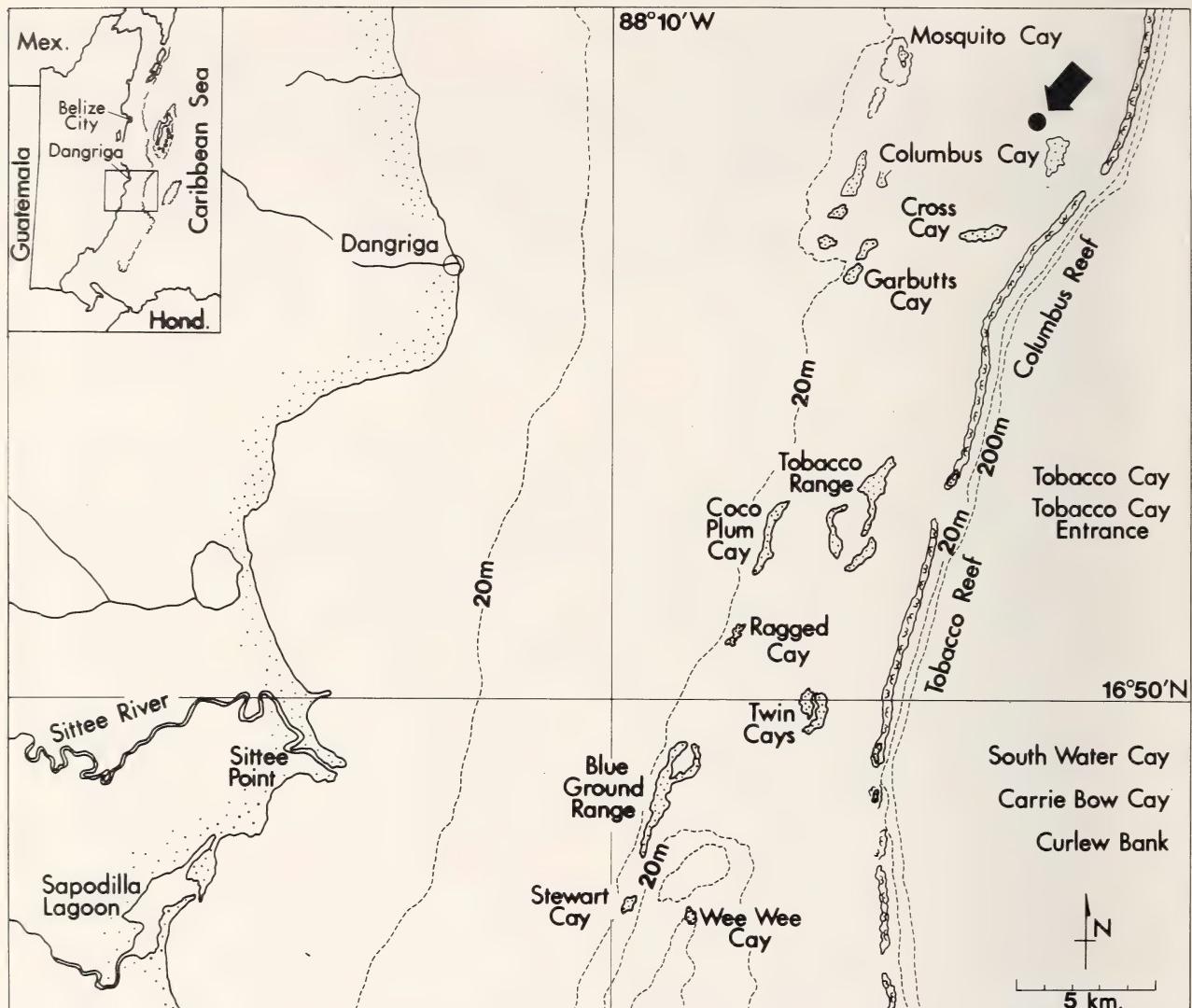


FIGURE 76.—Map showing location of submarine cave near Columbus Cay, Belize.

the smooth *Thalassia* meadow is a sand-filled sinkhole 200 m southeast of the cave (Figure 77). The sinkhole (50 m in diameter) has a smooth sandy bottom (10 m deep) that is ringed by a rich coral community established on rocky ledges and dominated by the corals *Montastrea annularis* (Ellis and Solander), *Acropora cervicornis* (Lamarck), *Diploria strigosa* (Dana), *Porites astreoides* Lamarck, *Porites porites* (Pallas), *Montastrea cavernosa* (Linnaeus), *Agaricia agaricites* (Linnaeus), along with the octocoral *Briareum asbestinum* (Pallas), and the sponges *Niphates digitalis* (Lamarck), *Iotrochota bir-*

*otula* (Higgin), and *Amphimedon compressa* (Duchassaing and Michelotti).

FIGURE 77 (opposite page, top).—Aerial view of location of submarine cave (sc) and sinkhole (sh); regularly spaced and aligned patches of bare sand in the *Thalassia*-covered lagoon delineate seismic shot-hole (ssh) patterns that have not been overgrown since seismic work was carried out here in the early 1960s; diameter of sinkhole in foreground is 50 m.

FIGURE 78 (opposite page, bottom).—Cave entrance; note sediment-laden algal mat (am) covering the surface sloping into the cave; water depth is 17 m.



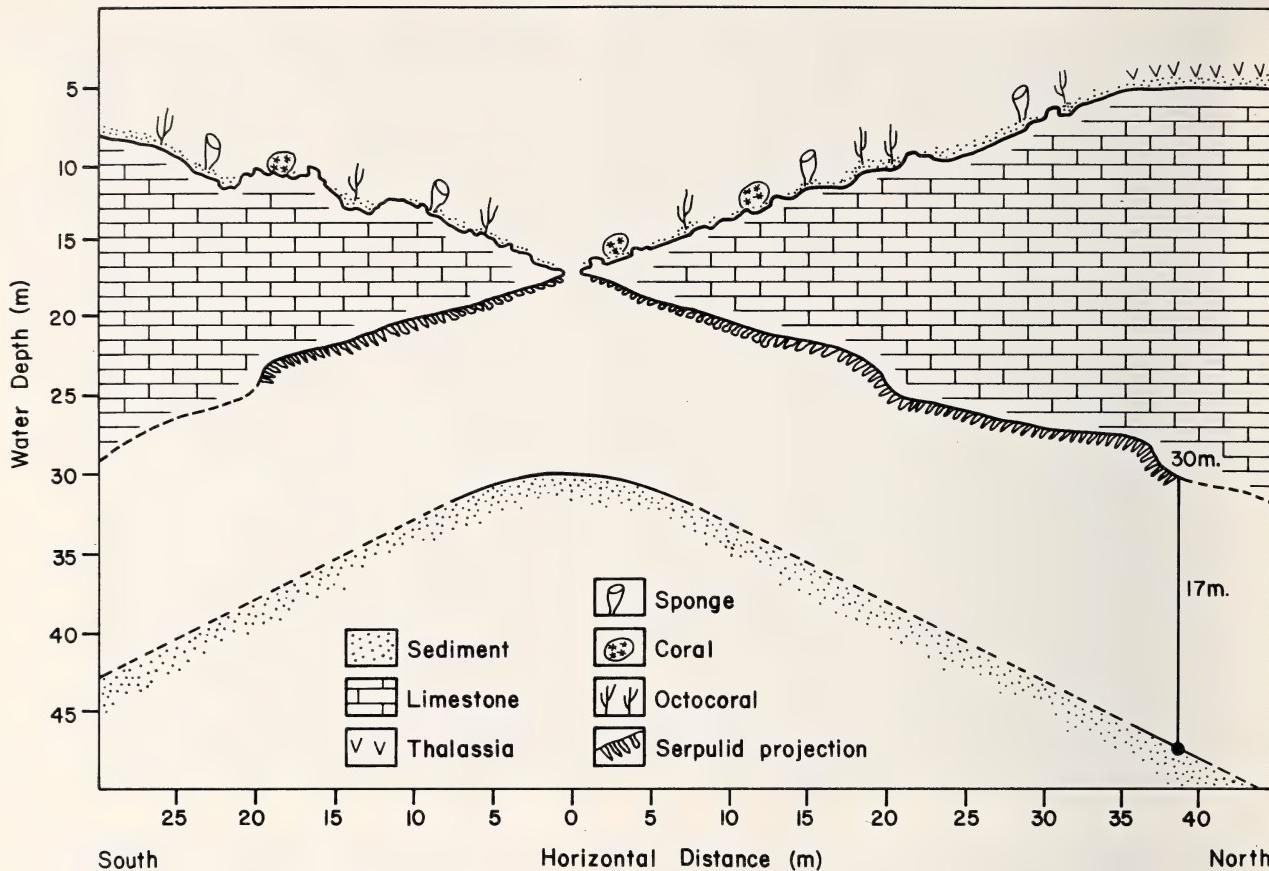


FIGURE 79.—Diagrammatic sketch of cave in cross section; note large sediment cone directly under cave entrance.

Interspersed in the *Thalassia testudinum* Banks ex König bed are several dense and large calcified green algae, mainly *Penicillus pyriformis* f. *explanatus* Boergesen and *Udotea wilsonii* Gepp and Howe ex A. and E. Gepp, with lesser amounts of *Halimeda simulans* Howe, *Rhipocephalus phoenix* (Ellis and Solander) Kützing, and *Penicillus pyriformis* A. and E. Gepp. Brown algae, however, are dominant among the coral heads, primarily *Dictyota bartayressii* Lamouroux, *Padina* sp., and *Lobophora variegata* (Lamouroux) Womersley (all Dictyotales; Dictyotaceae), as well as *Sargassum hystrix* J. Agardh (Fucales; Sargassaceae).

In contrast to the clear water and rich growth of corals at the sinkhole, the waters near the cave are turbid and the sea floor adjacent to the opening is covered by a few hardy scleractinian corals such as *Montastrea cavernosa*, *M. annularis*,

*Porites porites*, *Mussa angulosa* (Pallas), and *Scolymia* sp., together with the octocorals *Briareum asbestinum* and *Plexaura* sp., and some sponges typical of seagrass bottoms in the lagoon of the barrier-reef platform, branching *Aplysina fulva* (Pallas), *Amphimedon compressa* and *Iotrochota birotula*, vase-shaped *Niphates digitalis* and *Callyspongia vaginalis* (Lamarck) and massive *Ircinia strobilina* (Lamarck).

**ENTRANCE ZONE.**—An extensive sediment-laden, green algal mat up to 8 cm thick and 1–2 m wide surrounds the entrance to the cave at a depth of 17 m (Figure 78). The sediment is very fine sand to mud size carbonate containing an abundance of sponge chip material. The dominant algal component is the turf/mat-forming *Cladophoropsis membranacea* (C. Agardh) Børgesen (Siphonocladales; Siphonocladaceae), a siphona-

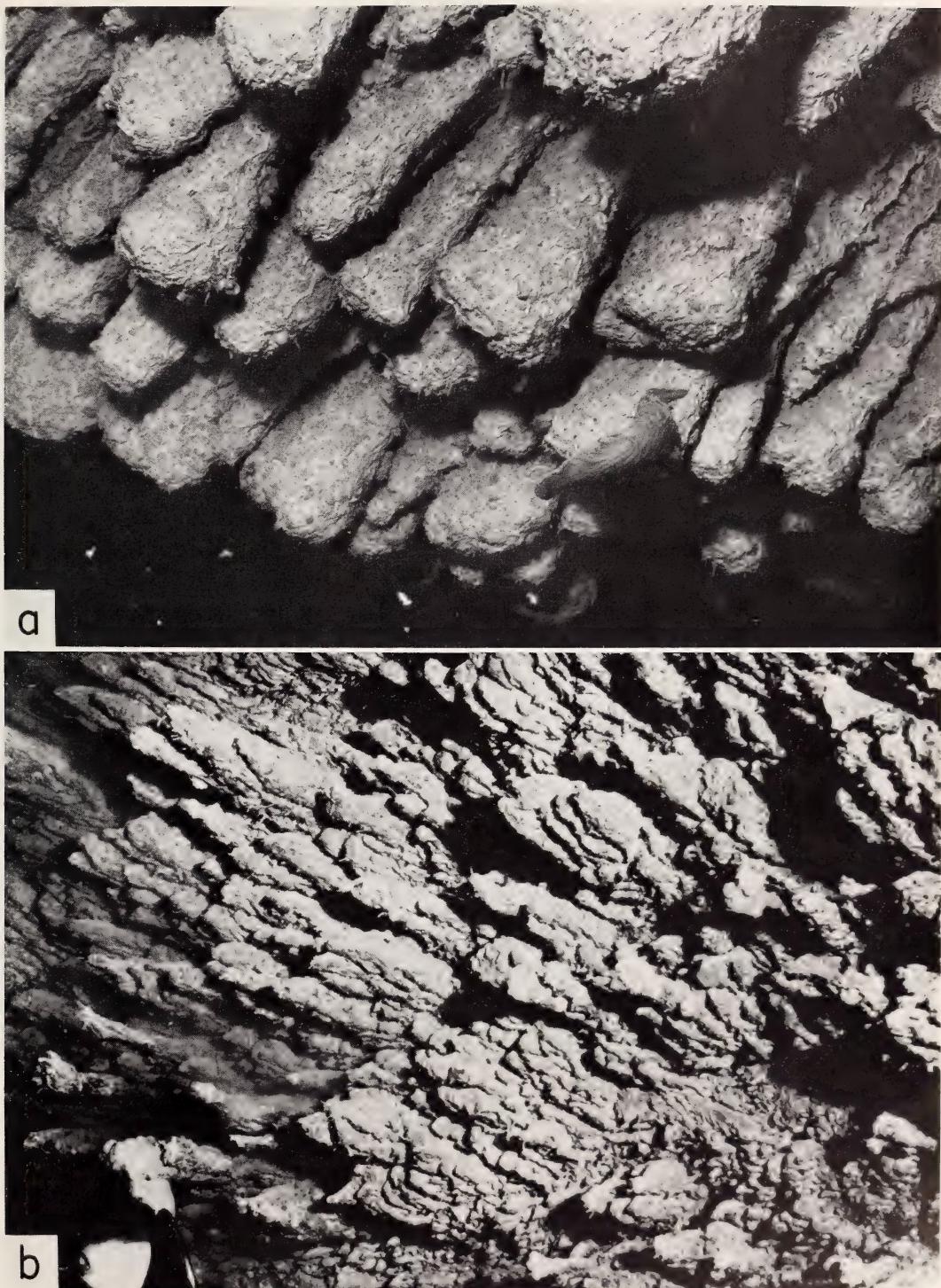
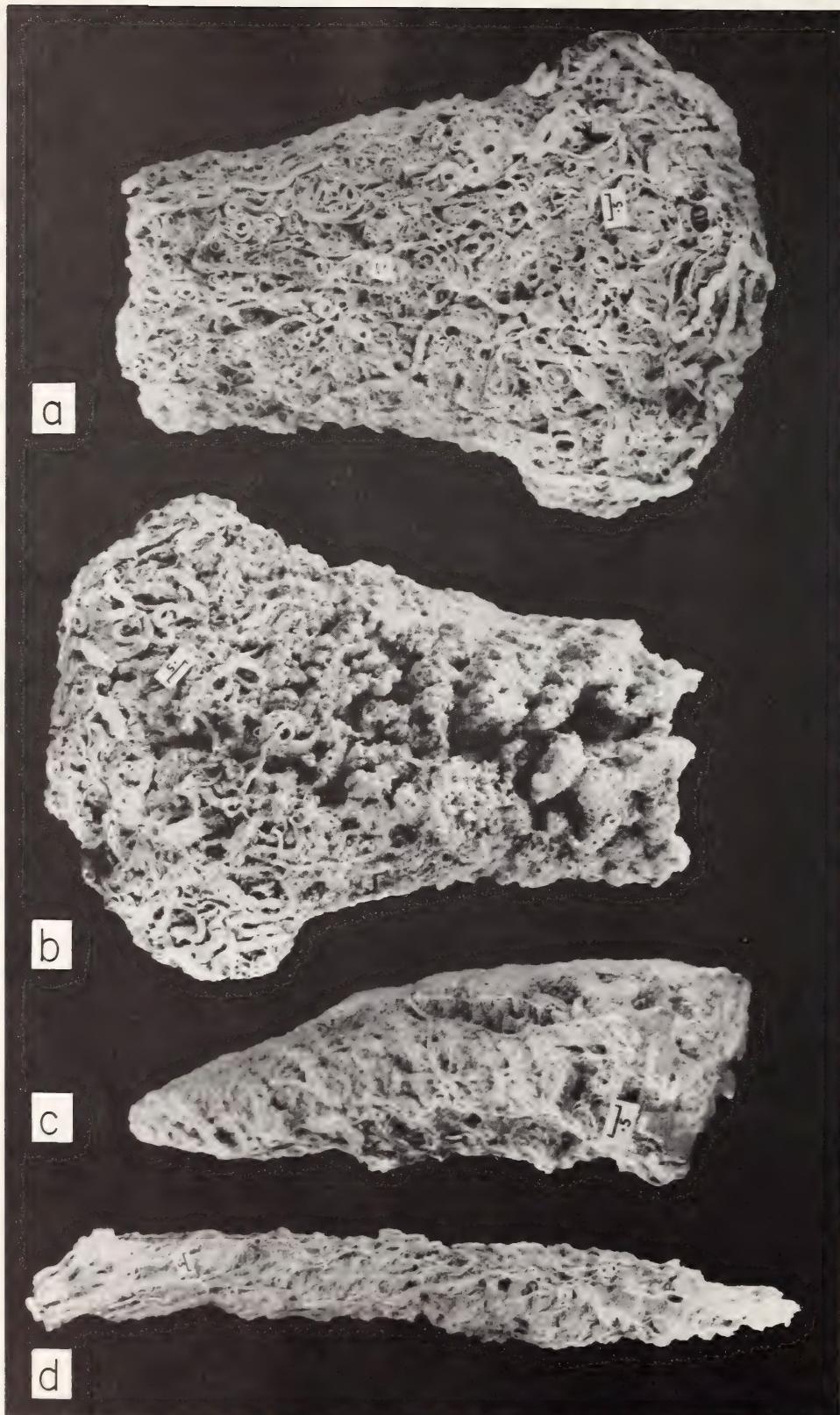


FIGURE 80.—Underwater views of pseudostalactites: *a*, club-shaped and steeply inclined projections 10 m from entrance, with conch shell fragment attached for settlement study; *b*, tapering and almost horizontal projections 20 m from entrance. (Each picture width = 1.5 m.)



ceous green alga (mainly unilaterally branched and having filaments up to 145  $\mu\text{m}$  in diameter) that typically occurs in the intertidal zone in calm water, where it can form extensive mats that sometimes become infiltrated with fine sand (Taylor, 1960; Kapraun, 1972). Because fine sediment clouds the water around the cave entrance at the slightest motion of water, it appears that the area is generally calm. Although suspended or gradually settling very fine sediment hampers visibility around the entrance, apparently enough light is still present to permit luxuriant algal growth, which may be enhanced by nutrients retained in the fine sediments.

Large schools of spadefish, *Chaetodipterus faber* (Broussonet), and permit, *Trachinotus falcatus* (Linnaeus), are common around the cave opening. In addition, a few cobia, *Rachycentron canadum* (Linnaeus), appear along with reef sharks, *Carcharhinus springeri* (Bigelow and Schroeder), which are known to use submarine caves as a retreat where they can rest undisturbed on the sediment floor (Clark, 1975).

**CAVE INTERIOR, GEOLOGY AND BIOLOGY.**—At a 17 m depth, the opening of the cave itself is no more than a large crack 3 m wide and 10 m long (Figure 78). The resulting poor light conditions within the cave as well as the considerable depth of water to which the cave descends makes it difficult to assess the overall size of the cave. At a point 40 m north from the opening, the cave-floor depth recorded on a line dropped to bottom was 47 m, which indicates a sharp slope away from the crest of the sedimentary cone located in depths of 30 m just below the opening (Figure 79).

The ceiling of the cave, covered by countless projections that are angled toward the opening, is a phenomenon only recently recorded in the

literature. These projections consist largely of serpulid tubes and magnesium calcite cement, and Macintyre and Videtich (1979) have named them "pseudostalactites" because they superficially resemble stalactites but are entirely of marine origin. The pseudostalactite cover begins about 3 m from the cave opening and extends for at least 40 m (the limit of our diving observations) at a water depth of 30 m (Figure 79). They slope toward the opening at angles varying from 40° to 60° near the opening to an almost horizontal orientation at the inner limit of observation.

These pseudostalactites are composed of serpulid tubes and varying amounts of microcrystalline magnesium calcite cement in and around tubes and infilling borings. Here and there, boring and subsequent lithification have resulted in extensive replacement of worm-tube framework by magnesium calcite cement. The largest pseudostalactites occur about 10 m from the opening of the cave and are distinctly club shaped, in some cases measuring up to 30 cm in width across the tip (Figures 80a, 81a,b). Within this area the pseudostalactites are dominantly serpulid aggregations and form an almost continuous field of tightly packed projections. In contrast, deeper into the cave, in addition to changing their angle, they become more widely spaced and progressively narrower, and the innermost surfaces observed are covered with almost pencil-thin projections (Figures 80b, 81c,d). The upper surface of most pseudostalactites consists of a layer of sediment-rich dense to chalky microcrystalline calcite. In general these sediment-rich calcite cappings are best developed on the innermost pseudostalactites observed (Figure 81c). Scanning electron photomicrographs show that this dominantly silt-sized sediment consists mainly of chips produced by boring sponges (Rützler, 1975).

The serpulid polychaetes partly responsible for these projections have been identified as members of two species of the *Vermiliopsis glandigera infundibulum* group (H. A. ten Hove, pers. comm. 1978), one of which is a thin-walled species commonly referred to in the Caribbean as *Vermiliopsis annulata* (Schmarda), and the other a thicker-walled species yet to be described (Figure 82a,b). Other

FIGURE 81.—Dried samples of pseudostalactites: a, lower surface of club-shaped projections (15 m from entrance) covered by serpulid tubes; b, upper surface of specimen in a showing knobs of calcite cement capping; c, side view of tapering projection (25 m from entrance) showing thick calcite cement coating over serpulid tubes; d, pencil-thin projection collected 40 m from cave entrance (limit of observation). (Scale = 0.5 cm.)

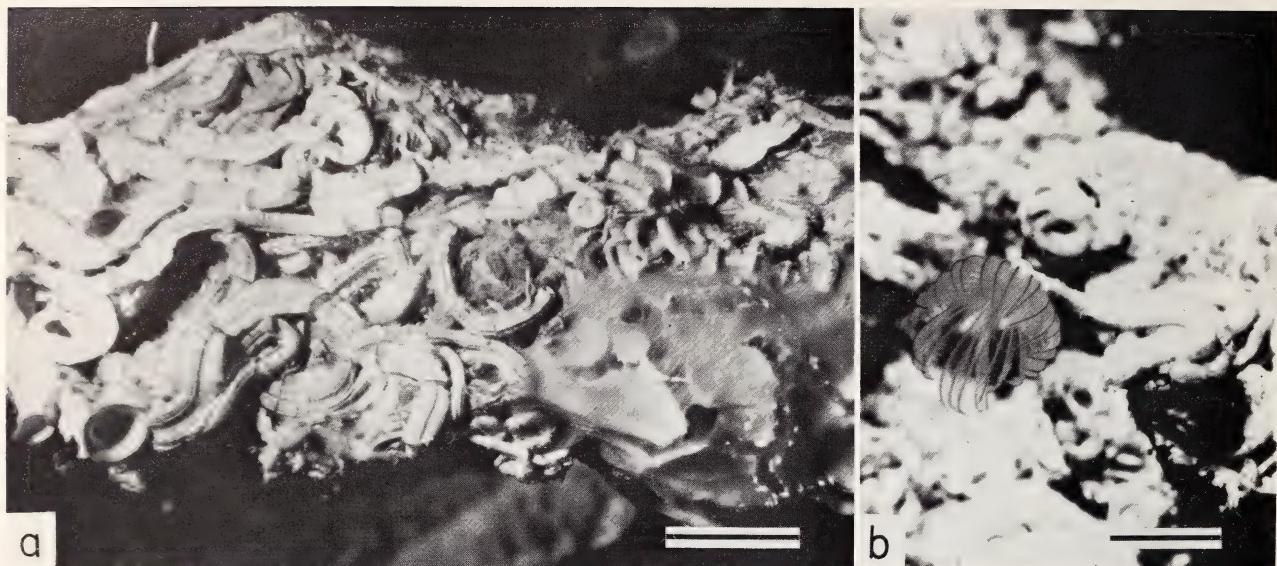


FIGURE 82.—Underwater close-up of pseudostalactite surfaces: *a*, *Vermiliopsis* spp. worm aggregation with sponge *Placospongia carinata*; *b*, live *Vermiliopsis* sp. with tentacle crown extended. (Scales = 10 mm.)

relatively common tubes, which are long and narrow, closely resemble those of *Metravermilia multicristata* (Philippi). There are also a few Spiorbinae tubes and some fine tubes of *Josephella marenzelleri* Caullery and Mesnic. Although the relative number of living serpulids could not be accurately ascertained, the lack of extended worms as well as a scarcity of worm-filled tubes in collected samples suggest that only about one percent of the surface tubes contain living serpulids.

In the poorly lighted to dark zone of the cave ceiling between 1 m and 20 m from the entrance, sponges are the most conspicuous associates of the serpulid projections. Samples from this area contained gray to white *Geodia gibberosa* Lamarck, some with drooping digitate processes (Figure 83a), a stringy yellow *Aplysina* sp., whitish cushions of *Chondrilla nucula* Schmidt, orange-brown cushions and crusts of *Placospongia carinata* Bowlerbank (Figure 82a), and whitish crusts of *Spirastrella coccinea* Duchassaing and Michelotti. Two other common whitish sponges belong to the Lithistida, encrusting *Desmanthus incrustans* (Topsent) and egg-shaped *Gastrophanella implexa*

Schmidt (Figure 83b). Small cryptic species, including *Microciona affinis* (Topsent), *Stellettinopsis* sp., and *Samus anonyma* Gray, coat and permeate dead serpulid worm tubes. The orange sclerosponge *Ceratoporella nicholsoni* (Hickson) (Figure 83a) is visible on a close-up photograph of the vertical surface of a break in the ceiling contour, but only a few minute specimens could be secured from a nearby location.

The dominant living mollusks found in association with the pseudostalactites for about 25 m from the cave entrance were the nestling arcid bivalve, *Barbatia dominensis* (Lamarck), and the encrusting venerids, *Chama congregata* Conrad and *Chama macerophylla* (Gmelin). Although boring bivalves are common in the pseudostalactites to the limit of our observations, to date none have been collected alive. Most of these bivalves are well lithified in their borings by magnesium calcite submarine cement. They include *Gastrochaena* sp., *Lithophaga nigra* (Orbigny), *Gregariella coralliphaga* (Gmelin), and *Coralliophaga coralliphaga* (Gmelin). The common occurrence of as many as three of these bivalves, one inside another, in the same bore hole, indicates that many of them



FIGURE 83.—Views of cave ceiling showing sponge population: *a*, *Geodia gibberosa* (15 cm long) projecting from ceiling and *Ceratoporella nicholsoni* attached nearby (arrow); *b*, *Gastrophanella implexa* (5 cm diameter).

prefer to occupy an extant boring rather than to form their own.

Other biota present in this habitat include trace occurrences of small and seldom freshly preserved bryozoan colonies belonging to eight species of cheilostomes: *Parellisina curvirostris* (Hincks), *Cribilaria radiata* (Moll), s.l., *Escharina pesanseris* (Smitt) (?), *Exechonella antillea* (Osburn), *Hippopodina fegeensis* (Busk), *Hippothoa flagellum* (Manzoni) (?), *Tremogasterina* cf. *T. perplexa* Cook, and *Hippoporina pertusa* (Esper). Specimens of ascidians collected belong to *Pyura* sp., possibly near *P. vittata* (Stimpson).

Several epizoic algae were found growing on the pseudostalactites near the cave opening (17 m depth), primarily the red algae *Spermothamnion investiens* (H. and P. Crouan) Vickers (Ceramiales; Ceramiaceae), and *Polysiphonia macrocarpa* Harvey in MacKay (Ceramiales; Rhodomelaceae). Some very small specimens of the green alga, *Cladophoropsis membranaceae* occur here and there, and a single specimen of the filamentous brown alga, *Sphaelaria* sp. (Sphaelariales; Sphaelariaceae), which was non-fertile and could not be identified to species, was also recorded. Some microscopic blue-green algae of *Calothrix* sp. (Nostocales; Rivulariaceae) were also found.

The thickness of the entire veneer of serpulid-calcite cement on the ceiling of the cave could not be determined, and individual projections could not be measured beyond 50 cm because they tend to coalesce as they increase in size. In several recessed areas, the veneer appeared to be poorly developed and the ceiling became a relatively smooth surface except for some rounded depressions that are probably solution cavities in the Pleistocene host limestone. Inverse steps in the relief of the ceiling resembling "false walls" to a diver also indicate that a thin Holocene cover is present. These steps mark areas where the roof slumped off during the formation of the cave in subaerial Pleistocene conditions. In addition, here and there vertical cones that are coated with small inclined pseudostalactites project from the ceiling (Figure 84). These cones are probably true Pleistocene stalactites. The prominence of this



FIGURE 84.—Large (1 m) vertical projection (probably true stalactite) with surface covered by inclined pseudostalactites.

Pleistocene stepped surface and the presence of the stalactites as well as solution cavities in recessed areas indicate that the maximum thickness of the serpulid-cement veneer is probably less than 1 m.

The crest of a large cone of sediment located in a depth of 30 m directly below the cave opening consists mainly of very fine sand to mud-sized sediment (Figure 79); it has a relatively smooth surface and shows no signs of current ripple marks. Some recognizable trails leading to a few empty *Strombus* shells, indicate an unsuccessful search for food after these animals fell through the cave opening. The fresh condition of these trails long after the death and decay of the

trapped gastropods suggest a lack of bottom currents strong enough to disturb the sediments on the cave floor. The flanks of this sedimentary cone slope away to unknown depths.

## Discussion

**CAVE BIOTA.**—Characteristics of the species composition of the sessile benthos of marine caves in the euphotic zone has long been known to differ considerably from that of benthos in surrounding light-exposed substrates. Early work on shaded communities in the Mediterranean (summarized in Riedl, 1966), was followed by studies of coral reef tunnels off Madagascar (Vasseur, 1974), but little attention was given to crypto-fauna of the Atlantic reef systems until the discovery of sclerosponges and of a characteristic brachiopod-sclerosponge community under overhangs and in caverns and tunnels on the fore-reef slope of Jamaica (Hartman and Goreau, 1970; Jackson et al., 1971). The distinctive character of the cave faunas is principally the result of decreased illumination—lack of light excludes fast-growing space competitors, mainly algae, and, in coral reefs, hermatypic hydrocorals, scleractinians, and octocorals. The available substrate inside a cave is generally well suited for colonization by sessile filter feeders because its ceiling and vertical walls prevent burial in sediment. Water circulation, however, must be sufficiently strong to ensure the renewal of food supplies and the transport of metabolic waste.

Whether complete darkness may be limiting for organisms that do not depend on photosynthetic processes is difficult to determine because low light levels in shallow-water environments commonly occur in association with poor water circulation. A few observations on dark but open-ended (and therefore well-ventilated) tunnels show that predominant sessile biota consist of sponges, serpulid polychaetes, and a few ascidians and foraminifers (Vasseur, 1974), as well as some ahermatypic corals, sessile or boring mollusks (*Chama* sp., *Lithophaga* sp.), and minute bryozoans (Rützler, unpublished observation from Ber-

muda). These data indicate that except for sponges, only a few representatives of a small number of sessile groups have adapted to complete darkness within the shallow-water environment. Dark caves in the Mediterranean having a deep (10–40 m) single entrance—and therefore poor water circulation—are reported to be colonized mainly by serpulid polychaetes, along with boring bivalves (*Lithodomus lithophagus* (Linnaeus)), scleractinians, and a few sponges (Laborel and Vacelet, 1959). From such accounts it appears that serpulid polychaetes can adjust more easily than most cave dwellers to both complete darkness and stagnant water conditions.

**DISTRIBUTION AND RECRUITMENT OF SERPULIDS.**—The dominant serpulids in the pseudostalactites of Belize are not typical colonial organisms, for each tube is the result of the activity of a single individual. The projections thus represent a series of discrete settlement events, but we do not know whether the serpulids mature in the cave and their successive generations are recruited locally, or whether the settlements represent invasions from the outside. Most of the common serpulids in the cave near Columbus Cay mature in about one year, and some reproduce the year round. As a result, if serpulids were recruited locally, distinct settlement surfaces would be difficult to identify. If recruitment was the result of a rare event—such as a major flushing of the cave—then these events should be recognizable in the projections. The distribution of live serpulids suggests local recruitment in that a few scattered individuals were alive when the projections were sampled, but there were not signs of sheets or groups of live animals.

The low percentage of live serpulids and other biota in an area of such impressive serpulid-tube aggregations does suggest the episodic development of this cryptic community, which is supported by observations from “Grotte de la Triperie” near Marseille (Vacelet, 1964). Vacelet found that the center ceiling and the entire blind-ending tunnel of a large subtidal grotto were azoic except for a cover of empty serpulid tubes of *Serpula concharum* Langerhans, *Pomatostegus*

*polytrema* (Philippi), and *Vermiliopsis infundibulum* (Linnaeus) on the walls and on the numerous stalactites present in that cave. During maneuvering at the end of August 1963, a submersible (Soucoupe Cousteau) that entered the grotto stirred up the water considerably. Subsequently, small but live serpulids that had been established in the normally azoic zones in mid-October, by mid-January were dead.

Because filter-feeding serpulids are rheotactic rather than phototactic, the orientation of the pseudostalactites toward the cave entrance on both sides of this elongate opening is probably related to current conditions rather than light conditions. The accumulation of fine sediment around the entrance of the cave, the preservation of tracks of deceased and decayed *Strombus* on the sediment floor, and the lack of any currents during diving observations suggest minimal current activity around the entrance and inside the cave. Apparently there is, however, enough movement of nutrient-rich water associated with the cave opening to influence the direction of serpulid growth. The abundance of clionid sponge chips on the upper surfaces of pseudostalactites and the apparent lack of excavating sponges in the cave indicate that the occurrence of temporary influxes of outside water capable of transporting this fine sediment into the cave.

**DISTRIBUTION OF CAVE SPONGES.**—Divers studying the ecology of shallow marine caves (0–5 m) in the Mediterranean have found large and diverse sponge populations whose composition differs significantly from that of sponges found on light-exposed rock substrates in similar depths. Qualitative and quantitative comparisons revealed that gradients of light, water movement, and inclination of substrate (exposure to sedimentation) are responsible for these zonation patterns. Sponges known from much greater depths (10s to 100s m) were also found in these shallow caves (Sarà, 1958, 1961; Russ and Rützler, 1959; Rützler, 1965, 1966). Similar findings have been reported in shallow reef tunnels in the Indian Ocean (Vacelet and Vasseur, 1965) and in deeper caves (4–25 m) in the Mediterranean (Pouliquen,

1972). Among the most interesting sponges collected from dark caves were live pharetronids (Vacelet, 1964; Vacelet and Vasseur, 1965) and sclerosponges (Hartman and Goreau, 1970). In addition, lithistid sponges common at bathyal depths elsewhere have been found in shallow caves in Madagascar (Vacelet and Vasseur, 1971) and in the Mediterranean (Pouliquen, 1972).

The sponge fauna in Columbus Cay cave differs considerably from that of the lagoon surrounding the entrance, which is similar to the fauna of other Caribbean lagoon habitats at similar depths, for example, near Carrie Bow Cay. Of the sponges in the cave, *Geodia gibberosa*, *Placospongia carinata*, and *Spirastrella coccinea* are species common elsewhere under rocks or back-reef rubble; *Chondrilla nucula* is one of the few sponges that grow abundantly either in full light, where it is olive to brown from symbiotic zoocyanellae, or in full darkness, where it is white to cream colored (Wilkinson and Vacelet, 1979); and *Aplysina* sp. has been collected only in caves, although morphologically it closely resembles species from illuminated habitats and ecologically it resembles *Verongia* (= *Aplysina*) *cavernicola* (Vacelet, 1959).

Little information is available on the cryptic species found in the cave. The absence of clinoids in the cave is surprising because most of the carbonate silt on the upper surfaces of the pseudostalactites is derived from these sponges. The lithistid that is present (*Desmanthus incrassans*) is known also from shallow caves in the Mediterranean and Indian Ocean; although its type specimen was dredged from the Campeche Bank, Gulf of Mexico (unknown depth), it has not since been reported from the western Atlantic (Vacelet et al., 1976). The other lithistid in the cave, *Gastrophanella implexa*, has not been found since its first description from west of Florida (180 m depth) and southwest of Cuba (230 m depth) (Schmidt, 1879:29). Although both sclerosponges and bathyal lithistids are now documented in Caribbean caves, no representative of the pharetronids has yet been found in these waters.

Whereas the serpulid pseudostalactites occur along at least 40 m of the ceiling of the cave,

sponges and the few other sessile biota present do not extend beyond the first step in the ceiling, which is less than 20 m from the entrance. Whether or not other openings occur in deeper parts of the cave and possibly admit water from the lagoon, the sponge population near the known entrance appears to receive an adequate supply of nutrient-rich water. This is probably introduced by waves, by the activity of resident or visiting fishes, or by some tidal flow through the small entrance. The inner zones of the ceiling may now and then receive renewed water containing nutrients and serpulid larvae as a result of upheaval during severe winter storms or even hurricanes.

**DISTRIBUTION OF ALGAE.**—The epizoic algae associated with the pseudostalactites near the entrance of the cave (17 m depth) are all filamentous, small in size, and sparsely distributed, and are typical of cryptic habitats as well as algal turfs, although elsewhere they generally occur in shallower depths.

**MINERALOGY OF PSEUDOSTALACTITES.**—Microprobe analyses indicate that the magnesium calcite cement, which commonly constitutes more than half of the pseudostalactites averages 15 mole percent  $MgCO_3$ . This composition together with the dentate crystals, peloidal texture, knobby surface relief, and minor amounts of acicular aragonite present in the pseudostalactites is characteristic of shallow-water submarine cements (Macintyre et al., 1968; Shinn, 1969; Land and Goreau, 1970; Ginsburg et al., 1971; Alexandersson, 1972; James et al., 1976; Macintyre, 1977). Oxygen and carbon isotope analyses indicate that fresh water did not influence the formation of these projections (Macintyre and Videtich, 1979). Thus, petrographic and geochemical data point to a marine origin for the cave cement.

Radiocarbon dates were obtained for two pseudostalactite samples: the core of a club-shaped specimen 5–10 m from the cave opening gave a date of  $820 \pm 60$  years B.P., and the dominantly Mg calcite cement cap of a specimen 25 m from the opening gave a date of  $650 \pm 40$  years B.P.

Because these dates are uncorrected, however, they may be less than true dates if bomb carbon is present. A slow accretion of the Holocene cave encrustation is confirmed by the lack of measurable encrustation over a one-year period on conch-shell fragments nailed to the ceiling at a distance 10 m from the opening. All the projections in the cave, including massive club-shaped formations near the entrance, appear to be accreting slowly. The date of the cement cap clearly indicates that even the thick crusts of cement may have developed over a long period of time. This finding is surprising in light of Goreau and Land's (1974) observation at a blast site in the deep fore reef of Jamaica. They found appreciable lithification within a period of one year.

The extensive cover of Mg calcite submarine cement on the ceiling of the cave confirms earlier observations that submarine lithification is most extensive in areas where little or no sediment accumulation occurs and where substrates are exposed for long periods of time (see Macintyre, 1977). Although similar cements have been well documented in a variety of marine habitats, the processes responsible for submarine lithification remain unidentified.

### Conclusion

The submerged Pleistocene cave in a *Thalassia*-covered lagoon of the barrier-reef platform off Belize is an unusual cryptic habitat having no known counterparts in other marine environments. The restricted flow of water in this cave has been more favorable to the establishment of serpulid worms than to other forms of encrusting fauna. Sessile biota, including sponges, filamentous algae, mollusks, and bryozoans are only minor constituents sparsely distributed on the ceiling of the cave over an area generally less than 25 m from the entrance. The serpulids, on the other hand, have formed massive projections superficially resembling stalactites (called pseudostalactites) that are inclined at decreasing angles away from the entrance and oriented toward the cave opening. These projections are present for at least 40 m from the opening, but their

shape changes gradually from club-shaped forms reaching 30 cm in width near the cave entrance to pencil-thin forms at the inner limit of our observation. The pseudostalactites are extensively

infilled and encrusted by submarine cement, which is a magnesium calcite cement similar to submarine cements reported elsewhere off Belize as well as in other tropical reef areas of the world.

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# Surface Zooplankton at Carrie Bow Cay, Belize

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## ABSTRACT

Zooplankton at Carrie Bow Cay, Belize, was sampled by conventional plankton net tows in the open ocean immediately seaward of the reef and in the lagoon in order to obtain plankton both before and after it had passed over the reef. Tows were taken at the surface and in depths of 3 m at each location, at approximately 0400 h, 0800 h, 1600 h, and 2000 h. The composition of the samples indicates primarily oceanic plankton at both locations, and elements of a presumed resident reef fauna at the shallower lagoon station. Results demonstrate a net import of zooplankton to the reef and substantiate observations by other workers that plankton abundance increases at night.

## Introduction

Investigations of zooplankton diversity, dynamics, and biomass provide essential information about breeding patterns (Moore and Sander, 1976, 1977), behavioral strategies (Emery, 1968; Alldredge and King, 1977), emergence patterns (Glynn, 1973; Porter, 1974; Porter et al., 1977), predation (Johannes et al., 1970; Goreau et al., 1971; Stevenson, 1972; Davis and Birdsong, 1973; Gerber and Marshall, 1974; Hobson, 1974; Porter, 1974), and the energetic impact of planktonic organisms on coral reef communities (Yonge, 1930; Sargent and Austin, 1954; Odum and Odum, 1955; Quasim and Sankaranarayanan, 1970; Tranter and George, 1972; Glynn, 1973; Johannes, 1974; Johannes and Gerber, 1974; re-

view by Lewis, 1977). The present report is concerned with zooplankton from the surface water adjacent to the coral reef at Carrie Bow Cay, Belize, and its possible import to that coral reef community.

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## Materials and Methods

Plankton was sampled by towing a 29 cm diameter plankton net (100  $\mu\text{m}$  mesh net, 250  $\mu\text{m}$  mesh basket) at a fixed distance behind a small boat during April and May 1976. In order to sample plankton both before and after it had passed over the barrier reef, the net was towed parallel to the reef at two locations. Site 1 ("ocean") is immediately seaward of the fore-reef slope. Water depth in this area is greater than 200 m. Site 2 ("lagoon") is approximately 0.5 km shoreward of the reef at Carrie Bow Cay. Water depth at site 2 ranges from 5 to 8 m. The predominant wind direction at the time was ENE, so that trade winds were blowing from the open ocean in the direction of the lagoon.

Horizontal tows at each site were taken consecutively at two depths, 0–0.5 and 2.5–3.0 m. Approximate times of tows were 0400 h (approximately 1 hour before sunrise), 0800 h, 1600 h and 2000 h (approximately 1.5 hours after sunset) during the same 24-hour period, whenever weather conditions permitted.

The net was equipped with a calibrated flow meter and all tows were timed (5–10 min) with a stopwatch, so that volume of water filtered could be calculated. Samples were fixed in 10% for-

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malin in sea water in the boat immediately after each tow. In addition, live samples were returned to Carrie Bow Cay for observation.

The settled volume of the plankton in entire samples was determined by straining samples through 100  $\mu\text{m}$  mesh plankton netting and rinsing them into a 25 ml graduated cylinder. Volume was recorded until constant readings were obtained (24 to 36 h). Large organisms such as Scyphozoa and Leptocephalus larvae (Pisces) as well as plant debris (for instance, *Thalassia testudinum* Banks ex König and *Turbinaria* sp.) were removed prior to volume determination. Any embryos suspended in mucus, however, could not be removed without interfering with other organisms in the sample.

All samples were then subdivided using an eight-chambered plankton splitter. The volume of each sample was adjusted to 100 ml by the addition of 10% formalin in filtered sea water prior to splitting. One-eighth of each sample was removed and stained with 0.1% rose bengal to facilitate identification and enumeration of organisms. The highly abundant copepods and non-cirripede nauplii (mostly copepod) were counted by adjusting the one-eighth subsample to a volume of 20 ml and further subsampling it by removing 1 or 2 ml with a Hensen Stemple pipette. All counts were made under a Wild M 5 stereomicroscope having a plankton counting wheel mounted on the base. The field of view at  $\times 25$  magnification spanned the width of the plankton wheel groove and permitted continuous counting while the wheel was rotated.

The remaining seven-eighths subsample was strained through 100  $\mu\text{m}$  mesh netting, dried at 60°C for 24 h and weighed to the nearest 1 mg after cooling in a desiccator. Samples were then ashed at 510°C and ash-free dry weights calculated.

The Wilcoxon signed-ranks test (Sokal and Rohlf, 1969) was applied to means generated exclusively from paired groups of samples.

## Results

Copepods and nauplii comprise much of the plankton in both lagoon ( $n = 40$ ) and ocean ( $n$

= 32) samples (Table 13). In the lagoon, copepods account for 53.0% and nauplii (mostly copepod) account for 31.5% of the total number of individuals (combined value = 84.5%). Similarly, in ocean samples the mean percentage of copepods was 52.7 and of nauplii 29.7 (combined value = 82.4%). At the taxonomic level at which the organisms were counted, more than 82% of the taxa were common to both lagoon and ocean samples. These values are comparable to those reported by Moore and Sander (1976) for the inshore zooplankton overlying two other Caribbean coral reef areas, where copepods comprised 76.0% (Jamaica) and 84.4% (Barbados) of the plankton.

Significant quantitative differences appear when samples are compared on the basis of the

TABLE 13.—Relative abundance (percentage of individuals) of major plankton categories ( $\geq 0.5\%$ ) on either side of the barrier reef at Carrie Bow Cay (number of samples in parentheses)

Plankton	Lagoon (40)	Ocean (32)
Copepoda	53.0	52.7
Nauplii	31.5	29.7
Gastropoda larvae	3.0	2.0
Fish ova	2.4	1.2
Larvacea	2.2	8.3
Polychaeta larvae	1.9	3.9
Shrimp* larvae	1.1	0.3
Brachyura larvae	1.1	0.3
Pteropoda	0.9	1.0
Cirripeda larvae	0.8	0.7
Chaetognatha	0.7	0.5

\* Euphausiacea, Penaeidea, Caridea.

TABLE 14.—Results of Wilcoxon signed-ranks test applied to abundance of organisms in different sample groups compared on basis of mean number of individuals/ $\text{m}^3$  (data from Table 15; + = significant at  $P \leq 0.05$ ; 0 = no significant difference)

Sample groups compared	Total plankton	Copepods and nauplii		Others
Ocean : Lagoon	+	+	+	
Night : Day	+	+	0	
0-0.5m : 2.5-3.0 m depth	0	0	+	

TABLE 15.—Summary statistics for counts and biomass values (means  $\pm$  standard error) for plankton of all lagoon and ocean tows (composite data from the two habitats are identified by hour, depth, and number of samples)

Statistic	Lagoon						
	0800 h		1600 h		2000 h		
0-0.5 m (n = 5)	2.5-3.0 m (n = 6)	0-0.5 m (n = 5)	2.5-3.0 m (n = 5)	0-0.5 m (n = 5)	2.5-3.0 m (n = 4)	0-0.5 m (n = 5)	
Volume filtered (m <sup>3</sup> )	28.5	24.4	30.1	28.7	27.3	26.3	26.9
Total no. of individuals/m <sup>3</sup>	485.4 $\pm$ 122.7	384.8 $\pm$ 65.3	284.4 $\pm$ 53.0	394.0 $\pm$ 48.1	442.2 $\pm$ 181.8	428.3 $\pm$ 178.8	445.2 $\pm$ 167.5
No. of copepods and nauplii/m <sup>3</sup>	442.6 $\pm$ 120.1	340.8 $\pm$ 61.2	238.8 $\pm$ 51.3	336.0 $\pm$ 46.0	362.6 $\pm$ 175.2	355.5 $\pm$ 166.3	384.6 $\pm$ 145.8
No. of individuals other than copepods and nauplii/m <sup>3</sup>	42.8 $\pm$ 6.4	44.0 $\pm$ 9.4	45.6 $\pm$ 5.9	58.0 $\pm$ 9.0	79.6 $\pm$ 15.9	72.8 $\pm$ 19.1	60.6 $\pm$ 22.2
Settled volume (ml/m <sup>3</sup> )	0.25 $\pm$ 0.05	0.21 $\pm$ 0.04	0.17 $\pm$ 0.03	0.19 $\pm$ 0.05	0.27 $\pm$ 0.05	0.20 $\pm$ 0.05	0.17 $\pm$ 0.02
Ash-free dry weight (mg/m <sup>3</sup> )	2.04 $\pm$ 0.51	1.58 $\pm$ 0.35	1.10 $\pm$ 0.24	1.87 $\pm$ 0.88	3.43 $\pm$ 1.32	1.67 $\pm$ 0.34	1.68 $\pm$ 0.23

Statistic	Ocean						
	0800 h		1600 h		2000 h		
0-0.5 m (n = 6)	2.5-3.0 m (n = 6)	0-0.5 m (n = 4)	2.5-3.0 m (n = 4)	0-0.5 m (n = 3)	2.5-3.0 m (n = 3)	0-0.5 m (n = 3)	
Volume filtered (m <sup>3</sup> )	27.7	27.5	27.9	30.0	30.2	30.9	30.6
Total no. of individuals/m <sup>3</sup>	455.8 $\pm$ 92.2	508.8 $\pm$ 185.4	946.8 $\pm$ 158.4	606.0 $\pm$ 110.4	2061.5 $\pm$ 1250.5	2098.0 $\pm$ 1340.2	471.7 $\pm$ 229.8
No. of copepods and nauplii/m <sup>3</sup>	279.8 $\pm$ 66.8	390.3 $\pm$ 152.2	703.8 $\pm$ 171.3	480.3 $\pm$ 111.0	1902.0 $\pm$ 1217.0	2033.3 $\pm$ 1366.1	356.0 $\pm$ 152.0
No. of individuals other than copepods and nauplii/m <sup>3</sup>	126.0 $\pm$ 54.5	118.5 $\pm$ 35.7	243.0 $\pm$ 123.8	125.8 $\pm$ 2.4	159.5 $\pm$ 33.5	64.7 $\pm$ 32.0	115.7 $\pm$ 78.3
Settled volume (ml/m <sup>3</sup> )	0.38 $\pm$ 0.14	0.35 $\pm$ 0.10	0.30 $\pm$ 0.06	0.28 $\pm$ 0.07	0.31 $\pm$ 0.16	0.34 $\pm$ 0.04	0.21 $\pm$ 0.13
Ash-free dry weight (mg/m <sup>3</sup> )	1.65 $\pm$ 0.39	1.71 $\pm$ 0.65	2.65 $\pm$ 0.52	1.11 $\pm$ 0.32	5.28 $\pm$ 1.92	3.15 $\pm$ 1.00	1.66 $\pm$ 0.95

TABLE 16.—Plankton categories, and number of individuals (means  $\pm$  standard error) per m<sup>3</sup> water for all lagoon and ocean tows (composite data from the two habitats are identified by hour, depth, and number of samples; + = present but <0.5 individuals per m<sup>3</sup> water)

Plankton category	Lagoon						0400 h
	0-0.5 m (n=5)	2.5-3.0 m (n=6)	0-0.5 m (n=5)	2.5-3.0 m (n=5)	0-0.5 m (n=5)	2.5-3.0 m (n=4)	
Cnidaria larvae	1.3±0.78	+	0.8±0.58	1.0±0.44	+	+	0.5±0.29
Medusae	0.9±0.42	+	0.7±0.16	1.2±0.27	0.9±0.79	0.6±0.21	0.7±0.64
Siphonophora	3.0±0.94	+	+	+	0.9±0.30	+	1.0±0.28
Ctenophora	+						
Platyhelminthes larvae	1.1±0.45	1.4±0.76	0.3±0.17	0.6±0.14	+	+	0.6±0.28
Polychaeta larvae	4.4±1.43	3.9±0.91	5.0±1.44	5.6±0.71	9.2±2.54	16.8±5.78	5.3±0.81
Polychaeta adults	0.5±0.36	+					
Sipunculida larvae	+	+	+	+	+	+	+
Bryozoa larvae	9.6±1.26	8.1±1.94	6.6±1.35	8.0±1.89	13.5±2.71	9.8±3.37	8.1±2.10
Gastropoda larvae	0.7±0.32	0.8±0.27	3.3±0.84	2.7±1.27	1.5±0.67	0.7±0.55	0.5±0.30
Pelecyopoda larvae	2.9±1.74	+	0.7±0.60	6.9±2.39	3.3±1.33	8.5±6.05	1.6±0.80
Pteropoda	1.0±0.54	+	0.5±0.34	2.3±1.44	+	+	+
Cladocera	+						
Ostracoda	320.5±103.05	231.2±41.72	126.4±23.24	193.1±27.17	210.6±112.5	250.9±95.57	154.6±38.96
Copepoda	122.5±38.78	109.5±26.11	113.6±30.31	142.9±34.47	142.5±57.04	144.9±54.88	133.4±50.47
Nauplii	0.6±0.36	1.1±0.54	8.2±5.93	0.6±0.23	2.0±0.66	2.1±0.77	1.0±0.72
Cirripeda larvae	+	+	+	+	0.8±0.61	+	+
Stomatopoda larvae	+						
Mysidacea	+	+	+	+	+	1.2±0.66	0.9±0.58
Cumacea	+	+	+	+	5.8±4.14	+	2.9±2.22
Amphipoda	+	+	+	+	1.0±0.78	+	0.5±0.29
Shrimp* larvae	0.9±0.29	2.4±0.83	+	+	12.5±3.84	6.6±2.60	2.6±0.66
Anomura larvae	0.9±0.67	9.7±5.67	+	0.5±0.20	2.1±0.89	2.8±0.83	4.1±1.54
Brachyura larvae	0.8±0.69	+	+	+	+	+	7.2±4.31
Echinodermata larvae	+						
Hemichordata larvae	+						
Urochordata larvae	+						
Salpa	+						
Doliolida	5.2±0.76	5.1±1.10	6.3±2.05	18.4±10.24	4.7±1.05	11.33±7.30	24.8±21.00
Larvacea	4.9±1.21	2.6±0.83	1.1±0.63	1.8±0.41	1.8±1.27	2.0±1.41	2.4±0.72
Chaetognatha	4.6±1.66	2.9±0.98	12.4±3.20	9.1±3.32	17.4±4.62	7.1±4.08	1.9±0.53
Fish larvae	+						0.6±0.21

TABLE 16.—Continued

Plankton category	Ocean					
	0800 h	1600 h	2000 h	0400 h		
-0.5 m (n=6)	2.5-3.0 m (n=6)	0-0.5 m (n=4)	2.5-3.0 m (n=4)	0-0.5 m (n=3)	2.5-3.0 m (n=3)	0-0.5 m (n=3)
Cnidaria larvae	5.6±3.44	3.7±2.00	1.6±0.55	1.7±0.24	0.7±0.05	0.6±0.32
+ Medusae	+ 2.2±0.90	+ 2.4±0.55	0.8±0.21 2.6±0.77	+ 1.7±0.37	+ 1.0±0.05	2.8±1.77 1.9±0.92
Siphonophora	1.8±0.80	3.8±2.29	1.3±0.65	0.7±0.55	+ + + + +	1.4±0.79
Ctenophora larvae	27.2±16.58	25.9±23.83	112.7±91.82	17.9±7.05	18.7±11.00	17.8±2.08
Polychaeta larvae	0.9±0.46	2.0±1.97	1.1±0.58	+ + + + +	0.6±0.43	+ + + + +
+ Sipunculida larvae	+ 1.0±0.87	+ 9.7±2.55	14.9±1.69	16.6±8.08	0.7±0.70	14.2±3.58
Bryozoa larvae	9.1±2.24	2.1±0.97	1.9±0.50	2.0±0.66	+ + + + +	23.3±9.70
Gastropoda larvae	0.5±0.20	2.2±1.39	9.2±2.69	12.0±7.40	5.5±1.15	1.2±0.05
Pelecyopoda larvae	8.3±7.16	2.8±1.32	1.4±0.55	1.0±0.58	+ + + + +	2.8±0.60
Pteropoda	5.9±5.11	+ 0.5±0.37	+ 273.5±125.92	247.2±92.87	0.5±0.38	0.5±0.38
Cladocera	2.8±1.32	+ 273.5±125.92	392.3±166.15	1307.0±798.55	0.8±0.47	1.6±1.31
Ostracoda	0.5±0.37	+ 116.90±47.66	311.8±98.03	572.3±395.40	118.1±798.32	1.7±1.69
Copepoda	202.8±48.22	118.6±18.36	233.2±45.45	829.4±547.78	236.8±114.09	344.2±212.15
Nauplii	116.90±47.66	+ 0.8±0.54	15.5±15.50	3.0±3.00	+ + + + +	119.2±40.93
Cirripeda larvae	0.8±0.54	+ 0.5±0.48	6.9±5.76	0.7±0.05	5.5±2.12	216.7±140.76
Stomatopoda larvae				0.6±0.55		1.9±0.62
Mysidacea				0.8±0.35		
Cumacea				+ + + + +		
Amphipoda				23.3±6.45	+ + + + +	
Shrimp* larvae	0.5±0.22	+ + + + +	0.6±0.28	1.4±0.72	2.5±1.28	0.8±0.77
Anomura larvae	+ + + + +	1.8±0.92 0.8±0.33	0.6±0.38 + + + +	+ + + + +	0.6±0.56 1.2±0.64 0.6±0.36	1.3±1.11 1.4±0.20 1.3±0.38
Brachyura larvae			1.0±0.77 0.6±0.28	22.2±14.80 0.7±0.05	1.2±0.64 0.6±0.36	1.9±0.99 1.3±0.38
Echinodermata larvae						1.3±0.18
Hemichordata larvae	+ + + + +	1.2±1.20 0.6±0.48	0.5±0.48	1.1±1.13	+ + + + +	
Urochordata larvae						
Salpa						
Doliolida	0.5±0.43	+ 56.2±24.46	48.4±38.14	47.1±22.34	0.5±0.38	0.7±0.60
Larvacea	1.9±0.70	2.5±1.04	4.8±1.10	3.3±1.68	39.2±29.18	56.7±36.69
Chaetognatha	4.8±1.79	2.0±1.01	32.6±31.91	2.3±1.62	2.5±0.75	3.6±1.22
Fish ova					9.8±7.80	3.1±1.56
Fish larvae					1.1±0.35	0.7±0.25

\* Euphausiacea, Penaeidae, Caridea.

mean abundance of organisms in different habitats and light periods (Table 14). In order to eliminate the influence of the dominant copepods and nauplii, these groups were tested as a separate category. Abundance of organisms in ocean samples is greater than in lagoon samples with respect to all three counts. Night tows (0400 h and 2000 h) yield a larger combined number of individuals than daytime samples (0800 h and 1600 h), as would be expected from the bimodal pattern of plankton emergence (near dawn and dusk) indicated by Glynn (1973). This difference does not hold, however, for organisms other than copepods and nauplii which show no significant quantitative difference between night and day. On the other hand, surface tows (0–0.5 m) differ significantly from 2.5–3.0 m tows only with respect to plankton other than copepods and nauplii.

These differences are not entirely reflected by settled volume or ash-free dry weights (Table 15). When mean values for settled volume generated by paired groups of samples are compared by the Wilcoxon signed-ranks test, significantly more plankton volume/m<sup>3</sup> is found in ocean samples than lagoon samples and, contrary to individual numbers, in day tows than in night tows ( $P \leq 0.05$ ). The latter result is probably due to the presence of significantly more siphonophores in day samples (see below). Depth of tow did not have bearing on volume of plankton. Ash-free dry weight, which is a more reliable estimate of biomass than settled volume, does not differ significantly when locations or times of day are compared (Table 17) using means generated by paired groups of samples (Table 15). Significantly more plankton biomass (mg/m<sup>3</sup>), however, is found at 0–0.5 m than in 2.5–3.0 m, regardless of location or time of day. The lack of agreement between these measurements of numbers of individuals and biomass probably reflects differences in the composition of the samples (Tables 13, 16) as well as patchiness or unevenness in zooplankton distribution. Patchiness is indicated by the large standard errors of means calculated for all counts and biomass measurements in the present study (Tables 15, 16). It should be noted, however, that mean ash-free dry weight (mg/m<sup>3</sup>) of

ocean samples is greater than that of lagoon samples, that of night samples exceeds that of day samples, and that of 0–0.5 m samples is greater than that of 2.5–3.0 m samples (Table 17).

The dominant organisms other than copepods and nauplii represented at both locations indicate a primarily oceanic plankton: larval polychaetes, gastropods, cirripedes, and shrimps (Euphausiacea, Penaeidea, Caridea) as well as pteropods, larvaceans, chaetognaths, and fish ova (Tables 13, 16). Of these groups, polychaete larvae, gastropod larvae, larvaceans, and chaetognaths are significantly more numerous in ocean than in lagoon samples ( $P \leq 0.05$ ). Similarly, larval cnidarians, platyhelminthes, bryozoans, pelecypods, and echinoderms, as well as siphonophores, ostracods, copepods, nauplii, salps, and doliolids are more numerous in ocean samples. Also, although the blue-green alga *Oscillatoria* (= *Trichodesmium*) sp. was not counted, it was observed to be a major component of the ocean but not the lagoon plankton. These results may indicate a net import of organisms to the reef because oceanic plankton is removed from the water column by the reef community. Similar findings are reported by Tranter and George (1972) at Kavaratti and Kalpeni atolls in the Laccadives, by Glynn (1973) at Puerto Rico, and by Johannes and Gerber (1974) at Eniwetok Atoll. In contrast, Motoda (1940) and Johnson (1949, 1954) found zooplankton to be less abundant in ocean waters than in lagoon waters. However, as pointed out by several au-

TABLE 17.—Carrie Bow Cay plankton biomass, expressed as ash-free dry weights (mg/m<sup>3</sup>  $\pm$  standard error) for the six major sample groups, with results of Wilcoxon signed-ranks test for paired groups (+ = significant at  $P \leq 0.05$ ; 0 = no significant difference)

Sample group	mg/m <sup>3</sup>	Wilcoxon test
Ocean	2.35 $\pm$ 0.41	0
Lagoon	1.85 $\pm$ 0.30	
Night	2.48 $\pm$ 0.41	0
Day	1.71 $\pm$ 0.25	
0–0.5 m	2.44 $\pm$ 0.41	+
2.5–3.0 m	1.75 $\pm$ 0.28	

thors (Alldredge and King, 1977; Porter and Porter, 1977; Porter et al., 1978; Rützler et al., 1980), plankton samples from the surface waters associated with coral reefs do not necessarily reflect the amount of plankton actually available to reef organisms. In the present study, certain groups of organisms (mysids, cumaceans, brachyuran larvae) are present in significantly ( $P \leq 0.05$ ) greater numbers per  $\text{m}^3$  in the lagoon. Also, the percentage of the plankton represented by these groups, together with adult polychaetes and shrimp larvae, is greater in the lagoon than outside the reef (based on data in Table 13, with the addition of lagoon versus ocean sample percentages for adult polychaetes, 0.2:0.04; mysids, 0.08:0.004; and cumaceans, 0.4:0.005). Similarly, the foraminiferan *Rosalina* (= *Tretomphalus*) sp. was recorded as abundant in lagoon but not in ocean samples. These results may indicate a significant difference in the composition of the plankton between the two localities. Hence, this difference may also reflect the presence of a resident reef fauna in the lagoon, represented by organisms that are at times considered demersal, such as adult polychaetes, mysids, cumaceans, shrimp larvae, and brachyuran larvae (Tranter and George, 1972; Sale et al., 1976; Alldredge and King, 1977; Porter and Porter, 1977). Such a resident reef fauna would be sampled only partially by the methods used in the present study and more likely would appear in samples from the lagoon, where water depth is only 5–8 m and small patch reefs are common. Similarly, differences in composition but not necessarily in biomass of lagoon and offshore plankton were found by Johnson (1954), Odum and Odum (1955), Bakus (1964), Tranter and George (1972), and Sale et al. (1976). This difference would indicate removal of oceanic plankton by reef organisms and replacement by a resident lagoon plankton (Emery, 1968).

Tows taken at 0–0.5 m and 2.5–3.0 m appear to have similar composition. Mysids, cumaceans, and fish ova were more abundant ( $P \leq 0.05$ ) at 0–0.5 m whereas pelecypod and anomuran larvae were more common in 2.5–3.0 m tows.

Comparing day and night tows, significantly more cnidarian larvae, siphonophores, platyhelminth larvae, sipunculid larvae and cladocerans appear in daytime (0800 h and 1600 h) tows. Crustacean groups (ostracods, mysids, cumaceans, amphipods, shrimp larvae, and anomuran larvae) as well as doliolids, however, are more abundant at night (0400 h and 2000 h). Results of this study agree, in general, with Emery (1968), Johannes et al. (1970), Glynn (1973), Porter (1974), and Renon (1977), who have noted both quantitative and qualitative differences between day and night samples of zooplankton over a variety of coral reefs. More specifically, Alldredge and King (1977) also report more ostracods, mysids, cumaceans, amphipods, shrimps, and decapod larvae in night tows than in daylight tows at Lizard Island on the Great Barrier Reef.

## Conclusions

Copepods and nauplii (mostly copepod) combined account for 84.5% and 82.4% of the zooplankton in lagoon and ocean samples, respectively, from Carrie Bow Cay. Other major groups of organisms represented at both locations (larval polychaetes, gastropods, cirripedes, and shrimp, as well as pteropods, larvaceans, chaetognaths, and fish ova) indicate a primarily oceanic plankton.

The relative abundance of mysids, cumaceans, adult polychaetes, and brachyuran and shrimp larvae in the lagoon may indicate partial sampling of a resident reef fauna in this habitat. Samples from the open ocean contain a significantly greater number of organisms (copepods and nauplii, as well as all others) per  $\text{m}^3$  water than those from the lagoon, and therefore suggest a net import of zooplankton to the reef. Plankton biomass, expressed by ash-free dry weight was greater in ocean, night, and 0–0.5 m samples than in lagoon, day, and 2.5–3.0 m tows.

Resident reef fauna will have to be sampled directly before final conclusions can be drawn about the impact of zooplankton on the energy budget of the coral reef community.

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# Plankton Diatoms (Bacillariophyceae) from Carrie Bow Cay, Belize

Paul E. Hargraves

## ABSTRACT

Seventy-three diatom taxa from the coastal waters around Carrie Bow Cay, Belize (Central America) were found in samples collected April/May 1977 and January 1978. *Chaetoceros*, *Rhizosolenia*, and *Coscinodiscus* were the most common genera. Six species are new records for the Caribbean region. Distinct differences exist between spring and winter diatom flora. Although numerous spore-forming species were found, resting spores were absent. Cultivation of more tropical diatoms is seen as an aid in solving problems in the systematics of tropical phytoplankton.

## Introduction

The species composition of plankton diatoms along the Caribbean coast, unlike that of coastal areas in temperate regions, is poorly known. For oceanic areas of the Caribbean more information is available because a considerable number of oceanographic cruises have included sampling for phytoplankton (for instance, Hargraves et al., 1970; Hulbert, 1968; Marshall, 1973; Takano, 1960). Coastal floristic works are few and widely scattered geographically (Buchanan, 1971; Margalef, 1957, 1968; Sander, 1976). Apparently no publications deal with coastal plankton diatoms of Belize, although planktonic coccolithophorids have been examined (Kling, 1975).

In terms of turnover rate and primary production in tropical waters, the nanoplankton (larger

than 1–10  $\mu\text{m}$  but smaller than 50–70  $\mu\text{m}$ , depending on authors' definition) is often more important than the net plankton (Malone, 1971; Texeira, 1963); nanoplankton may occasionally dominate the biomass as well (Garrison, 1975). Owing to my limited sampling, the annotated list below does not completely represent plankton diatoms of Carrie Bow Cay. Also, primarily benthic species are excluded from this report, except for the few whose consistent presence indicates a pelagic as well as benthic existence.

Generally, diatom species have been defined on the basis of morphological characteristics without a proven genetic basis. Variability within a species is often considerable, not only morphologically (for example, Van Landingham, 1967, lists over 100 synonyms for *Actinocyclus ehrenbergii* that were formerly considered species, differentiated on morphological bases), but physiologically as well (for example, Carpenter and Guillard, 1971; Hargraves and Guillard, 1974). Although impractical for routine purposes, genetic analysis by means of enzyme electrophoresis (Gallagher, 1979; Murphy and Guillard, 1976) shows considerable promise for separating diatom species. Nevertheless, morphological features are the main criteria for current classification schemes.

The grouping of species into genera, of genera into families, and of families into orders is in a state of flux, primarily because of recent discoveries about fine structure of the siliceous diatom frustule (see reviews in Werner, 1977). Organization of these hierarchies is subjective, depending on individual assessment of the relative importance of given structures, and diatomists have

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probably not yet attained a wholly natural classification system. For this reason, the list below is arranged in alphabetical order rather than in a particular phylogenetic scheme. Some recent attempts at an incisive phylogenetic arrangement have been reviewed by Hendey (1974) and Simonsen (1974).

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### Methods

Samples were collected with 30 cm diameter plankton nets, having mesh sizes of 65  $\mu\text{m}$  or 10  $\mu\text{m}$  and were preserved in hexamine-buffered formalin or Lugol's iodine, without acetic acid. Aliquots were washed with distilled water to remove salts. To remove organic matter, cells were oxidized by either boiling for one hour in 30% hydrogen peroxide, or by ashing samples for three hours on cover slips on a hot plate. Permanent slides of the oxidized material were prepared using Hyrax (Custom Research & Development, Inc., Auburn, California) as a mounting medium. These permanent mounts and the liquid-preserved material were examined in a Zeiss Photomicroscope II using brightfield, phase contrast, and Nomarski interference contrast optics. When necessary, identifications were confirmed using a Cambridge Stereoscan electron microscope. Slides are maintained in the author's collection.

Collection sites were in the vicinity of Carrie Bow Cay, in the central portion of the Belize barrier reef. Surface tows were made over *Thalassia*, near the mangrove forests of Twin Cays, in the channel between Carrie Bow Cay and South Water Cay, in deeper water (over 200 m) about 0.5 km east of Carrie Bow Cay, and in the "Southern Shelf" of the lagoon, at approximately 16°55'N, 88°12'W in over 20 m depth. The samples were collected in April and May 1977 and January 1978 at the same localities, and thus they cover the late spring and mid-winter periods.

### Annotated List of Diatoms

(Species new to the Caribbean flora are designated by \*)

*Actinocyclus ehrenbergii* Ralfs in Pritchard (Figure 87a)

[= *A. octonarius* Ehrenberg]

Found only in lagoon samples in spring; never common. Previously reported from the Caribbean by Hagelstein (1938) and Margalef (1968). Characteristic of both benthic and pelagic environments. Reference: Hendey (1964).

*Actinocyclus subtilis* (Gregory) Ralfs in Pritchard

Found only in lagoon samples in spring; never common. Previously reported from the Caribbean by Hagelstein (1938) and Margalef (1968). Characteristic of both benthic and pelagic environments. Reference: Hendey (1964).

*Actinoptychus senarius* (Ehrenberg) Ehrenberg

[= *A. undulatus* (Bailey) Ralfs in Pritchard]

Found only rarely in samples from the lagoon side of Carrie Bow Cay in winter. A cosmopolitan species, it is widespread in temperate coastal waters in all seasons, but apparently rarer in the tropics. Reported from the Caribbean by Hagelstein (1938) and Margalef (1968) among others. Reference: Hendey (1964).

*Asterionella notata* (Grunow) Grunow in Van Heurck (Figure 85d)

Uncommon to common in all samples; more abundant on the ocean side of Carrie Bow Cay. A tropical coastal species straying rarely into temperate waters. Widespread in the Caribbean, but apparently misidentified occasionally as *A. kariana*, an Arctic species. Reference: Hustedt (1931-1959).

\**Asteromphalus hookeri* Ehrenberg (Figure 85c)

Present rarely and only in spring from the ocean side. Normally oceanic in cooler waters. Not previously reported from the Caribbean. Reference: Lebour (1930).

*Bacteriastrum comosum* Pavillard

Occasionally found in winter only in lagoon

and ocean-side samples. A predominantly tropical species, previously reported from the Caribbean by Margalef (1968). Reference: Hustedt (1927-1930).

#### *Bacteriastrum delicatulum* Cleve

Found in lagoon and ocean-side samples in spring and winter. An oceanic species, reaching its maximum abundance in temperate waters. Widespread and occasionally abundant throughout the Caribbean. Reference: Hendey (1964).

#### *Bacteriastrum elongatum* Cleve (Figure 86b)

Found rarely in ocean-side tows and only in spring. Commonly found in tropical waters, and widely reported from the Caribbean. Reference: Hendey (1964).

#### *Bacteriastrum cf. furcatum* Shadbolt (Figure 86a)

This cell was seen in one sample from the ocean side in spring. It resembles *B. furcatum* Shadbolt, sensu Boalch (1975), but insufficient material was found to make an identification.

#### *Bacteriastrum hyalinum* Lauder (Figure 85a)

Occasionally found in winter samples, from both lagoon and ocean side. Common in temperate and tropical coastal waters. Previously reported from the Caribbean by Hargraves et al. (1970) and Margalef (1968). Reference: Hendey (1964).

#### *Bacteriastrum varians* Lauder

Found once in a spring sample from the lagoon side of Carrie Bow Cay. Generally considered a tropical oceanic species, it was reported in the Caribbean by Takano (1960). Boalch (1975) considers *B. varians* a synonym of *B. furcatum* Shadbolt. Reference: Boalch (1975).

#### *Cerataulina pelagica* (Cleve) Hendey

[= *Cerataulina bergenii* (Péragallo) Schutt]

Present in small numbers in winter samples. Widely distributed in coastal temperate and tropical regions. Found throughout the Caribbean region. Reference: Hendey (1964).

#### *Chaetoceros affine* Lauder

Occasionally present in ocean-side samples in winter and spring. Widely distributed in tem-

perate and tropical coastal waters. Commonly reported from the Caribbean. The morphology of this species is highly variable. Some chains appear transitional to *C. diversum* and *C. laciniosum*. Single cells are also seen rarely. Reference: Hustedt (1927-1930).

#### *Chaetoceros atlanticum* Cleve

Very rare in ocean samples in both winter and spring. A widespread oceanic species in temperate and tropical waters. Reported from the Caribbean by Margalef (1968), Roukiyainen et al. (1973), and Sander (1976). The variety *neapolitana* seems more common to tropical waters. The morphology of some chains resembles *C. laciniosum*, from which it can be distinguished by the multiple chloroplasts and central tubule of the valve. Reference: Hustedt (1927-1930).

#### \**Chaetoceros boreale* Bailey

Rarely found in a spring sample on the ocean side of Carrie Bow Cay. This rather distinctive species is normally found in temperate or cold waters. It has not been reported previously from the Caribbean. Reference: Hustedt (1927-1930).

#### *Chaetoceros coarctatum* Lauder

A rarely found species from ocean-side samples in winter and spring. Generally found in the tropics, occasionally in temperate waters. Previously reported from the Caribbean region by Hargraves et al. (1970), Margalef (1968), and Takano (1960). Rarely vorticellid protozoans are attached to several cells in a chain. Reference: Hustedt (1927-1930).

#### *Chaetoceros compressum* Lauder

Only seen once in a winter sample. This species is normally considered a coastal species from temperate or boreal waters. Nevertheless, it is widely reported from the Caribbean, sometimes as a dominant species (Sander, 1976). Reference: Hustedt (1927-1930).

#### *Chaetoceros curisetum* Cleve

Occasionally seen in spring, but only in samples from the ocean side of Carrie Bow Cay. Widely distributed in coastal waters in temperate and tropical regions. Reported by most

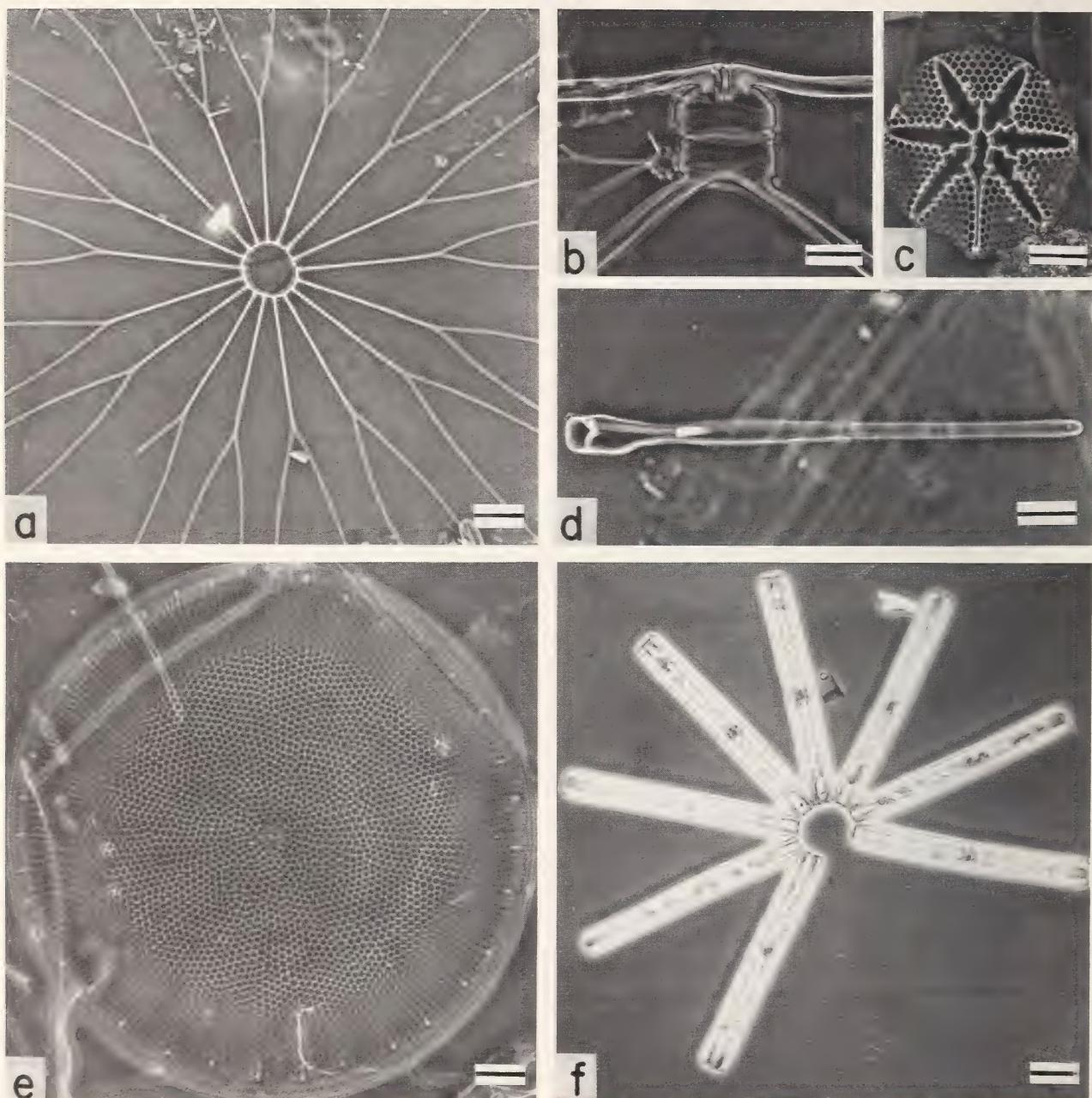


FIGURE 85.—Light photomicrographs of representative diatoms: *a*, *Bacteriastrum hyalinum*, valve view of cell with 17 setae (Hyrax mount); *b*, *Chaetoceros peruvianum*, girdle view of entire cell (only bases of setae are shown; Hyrax mount); *c*, *Asteromphalus hookeri*, valve view of cell (Hyrax mount); *d*, *Asterionella notata*, isolated cell in valve view (Hyrax mount); *e*, *Coscinodiscus jonesianus*, valve view (Hyrax mount); *f*, *Thalassionema nitzschoides*, eight-celled colony in girdle view (living material). (Scale = 10  $\mu\text{m}$ .)

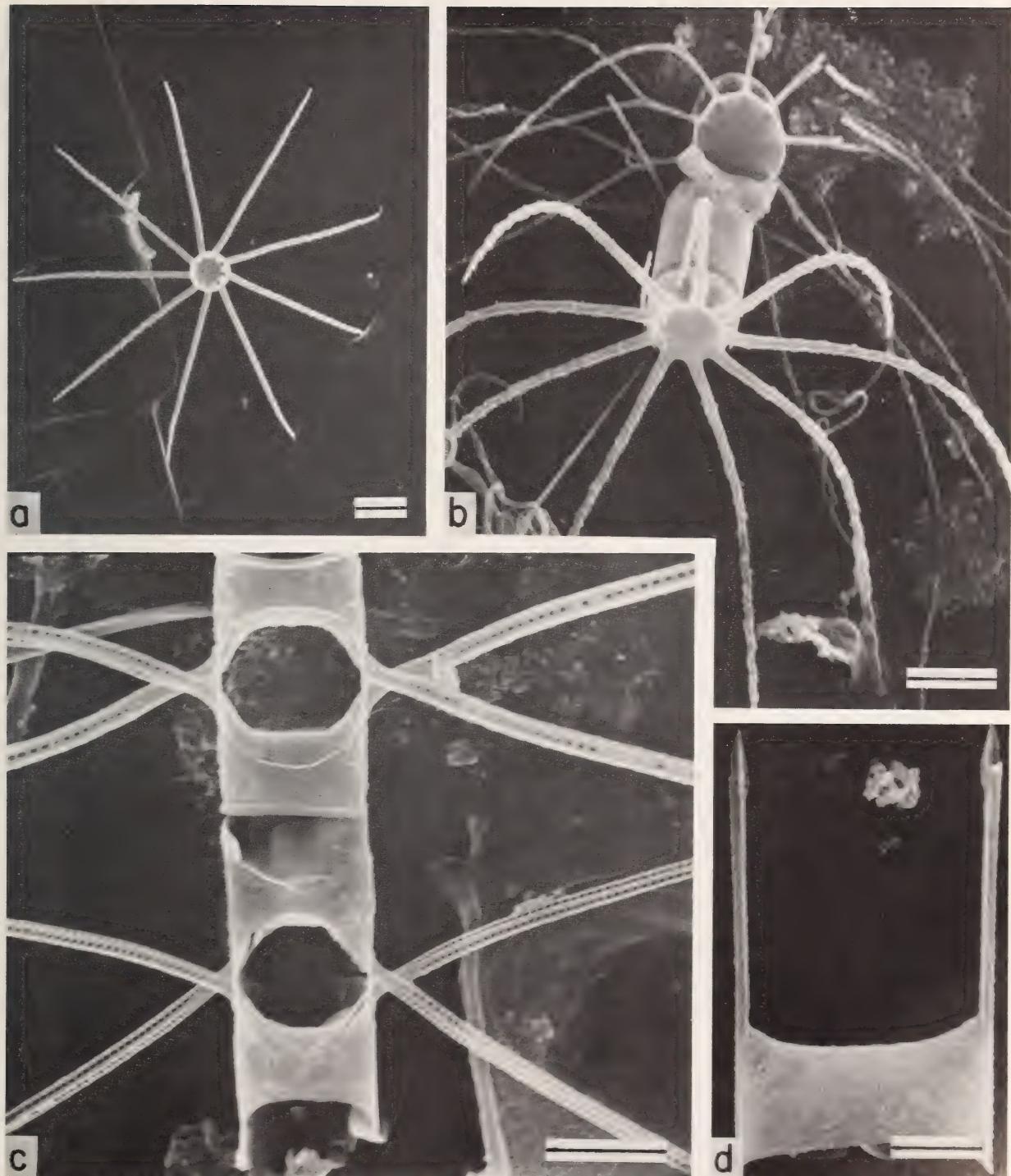
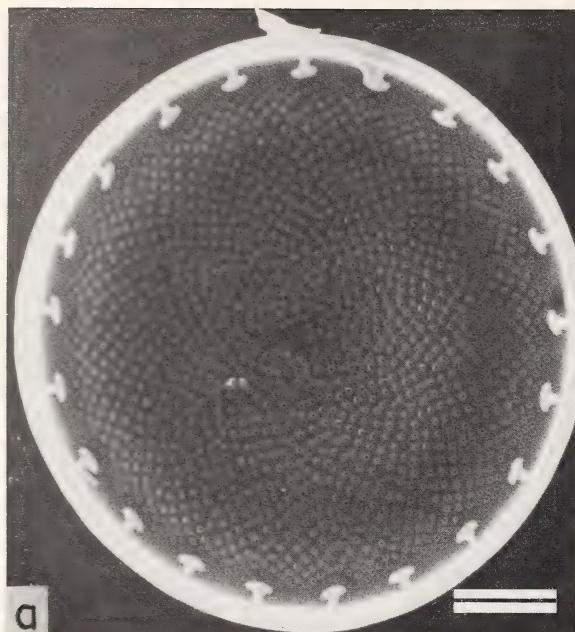
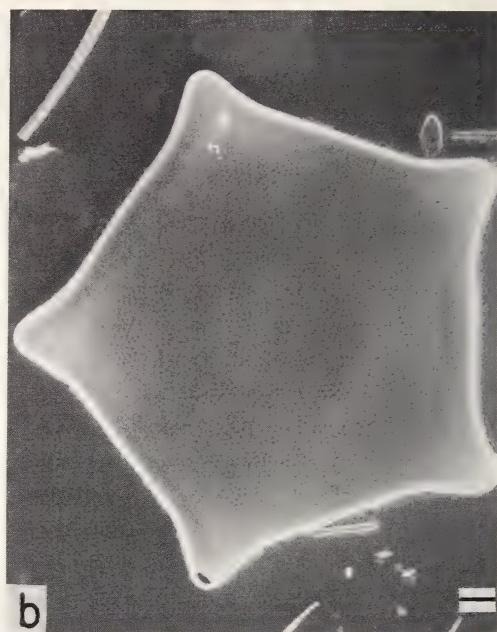


FIGURE 86.—Scanning electron photomicrographs of representative diatoms: *a*, *Bacteriastrum* sp., probably *B. furcatum* (sensu Boalch, 1975), valve view of terminal cell; *b*, *B. elongatum*, terminal and interior cells of a chain; *c*, *Chaetoceros lorenzianum*, girdle view; *d*, *Hemialus hauckii*, girdle view of an isolated valve. (Scale = 10  $\mu\text{m}$ .).



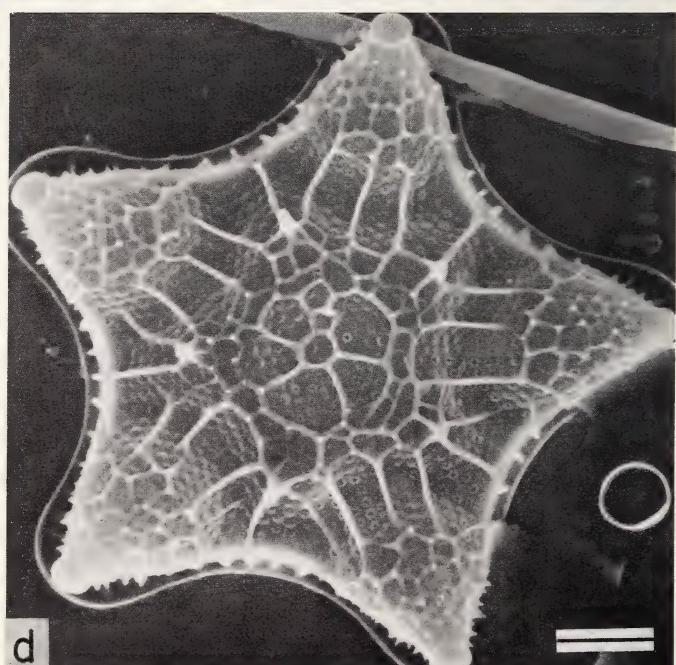
a



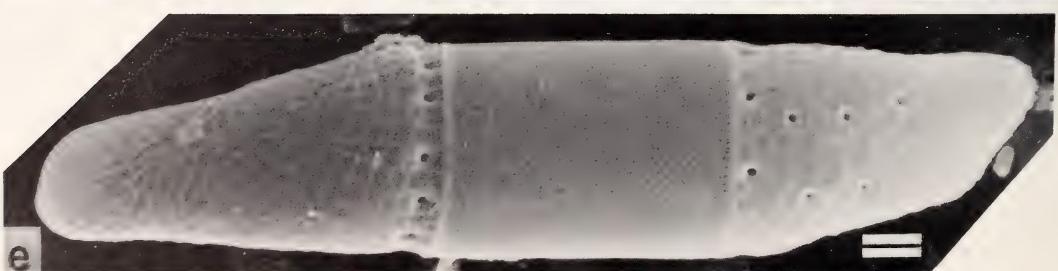
b



c



d



e

authors throughout the Caribbean. Reference: Hustedt (1927-1930).

*Chaetoceros danicum* Cleve

Occasionally found in lagoon samples in winter. Normally characterized as a temperate species favoring somewhat reduced salinity. Previously reported from the Caribbean by Margalef (1968) and Sander (1976). Reference: Hustedt (1927-1930).

*Chaetoceros decipiens* Cleve

Rarely observed in winter samples from the lagoon and ocean side of Carrie Bow Cay. Nominally an oceanic species from temperate and boreal waters, it has been previously reported from the Caribbean by most authors. The morphology of the species is variable; the distinctive features distinguishing it from *C. lorenzianum* are the nature of fusion of the setae and the presence of resting spores in *C. lorenzianum*. Fusion of the setae is a somewhat unreliable character in nature, and spores are rarely seen; it is possible that misidentifications have occurred, particularly in the case of narrow cells and short chains. Minor differences between the two are apparent at the ultrastructural level (Evenson and Hasle, 1976). Reference: Cupp (1943).

*Chaetoceros didymum* Ehrenberg

Fairly common in ocean-side samples in both spring and winter. Widely distributed in temperate and warm waters; also widely distributed in the Caribbean. Reference: Hustedt (1927-1930).

*Chaetoceros diversum* Cleve

Found in winter and spring in most samples. Considered to be a tropical coastal species, it is occasionally reported also in temperate waters. Previously reported from the Caribbean by Sander (1976) and Takano (1960). This species is easily confused with *C. laeve* Leu-

diger-Fortmorel and perhaps the two should be synonymous. Sander and Takano include both these species in their lists. Short chains may resemble *C. affine*. Reference: Cupp (1943).

*Chaetoceros laciniosum* Schutt

[= *C. distans* Cleve]

Occasionally present in ocean-side samples in spring. This species is common and widely distributed in temperate waters but also occurs in the tropics. Previously reported from the Caribbean by Hulbert (1968) and Sander (1976), the latter as "dominant." *Chaetoceros laciniosum* is another highly variable species, and in its growth forms can resemble *C. pelagicum* Cleve and *C. breve* Schutt. Superficially some chains also resemble *C. affine* and narrow forms of *C. atlanticum*. Reference: Hustedt (1927-1930).

*Chaetoceros lorenzianum* Grunow (Figure 86c)

Found in most samples in winter and spring. A common coastal form from temperate waters, it also is widely distributed in the tropics. It is widely reported, sometimes in abundance, from the Caribbean. Narrow chains particularly can be confused with *C. decipiens* (see comment for that species). Reference: Hustedt (1927-1930).

*Chaetoceros pendulum* Karsten

Seen once in a spring tow from the ocean side. A fairly rare oceanic species characteristic of tropical waters. Reports from the Caribbean by Sander (1976) and Takano (1960). Reference: Cupp (1943).

*Chaetoceros peruvianum* Brightwell (Figure 85b)

Found in a spring tow from the ocean side. A very common and widely distributed species in temperate and tropical waters, although rarely abundant. Present in both coastal and oceanic areas. Widely reported from the Caribbean (for instance, Sanders, 1976; Takano, 1960), as short chains and single cells. Reference: Cupp (1943).

*Chaetoceros pseudocurvisetum* Mangin

Occasionally in winter samples. A coastal species widely distributed in temperate and trop-

FIGURE 87.—Scanning electron photomicrographs of representative diatoms: *a*, *Actinocyclus ehrenbergii*, interior side of a small specimen; *b*, *Trigonium formosum*, external side of a five-sided form; *c*, *Rhizosolenia calcaravis*, side view of the valve; *d*, *Triceratium pentacrinus*, external side; *e*, *Isthmia enervis*, girdle view of the entire cell. (Scale = 10  $\mu\text{m}$ .)

ical areas, previously reported from the Caribbean by Hagelstein (1938), Margalef (1968), and Takano (1960). Reference: Cupp (1943).

#### *Chaetoceros tortissimum* Gran

Seen only once in a winter tow on the ocean side of Carrie Bow Cay. This is a characteristically temperate coastal species only occasionally seen and rarely of any abundance. It has been reported from the Caribbean by Margalef (1968) and Takano (1960). Reference: Hendey (1964).

#### *Climacodium biconcavum* Cleve

Rare; observed in only one tow from the ocean side in spring. A widely distributed tropical oceanic species. Previously reported from the Caribbean by Sander (1976) and Takano (1960). Reference: Hustedt (1927-1930).

#### *Climacodium frauenfeldianum* Grunow

Fairly common in the spring in both lagoon and ocean-side samples. Like *C. biconcavum*, this species is found only rarely outside the tropics, but it is apparently more common than *C. biconcavum*. The shape of the intercellular aperture is apparently the only distinguishing characteristic between the two species: elliptical or quadrate in *C. frauenfeldianum*, lanceolate or diamond-shaped in *C. biconcavum*. Sander (1976) and Takano (1960) have reported it in Caribbean waters. Reference: Cupp (1943).

#### *Coscinodiscus asteromphalus* Ehrenberg

Occasionally seen in ocean tows in the spring and lagoon samples in the winter. This is one of the most common *Coscinodiscus* species in temperate coastal waters. It is morphologically variable and may be confused with other species, and has rarely been reported from the tropics. The only previous Caribbean record is Hargraves et al. (1970). Reference: Hustedt (1927-1930).

#### *Coscinodiscus centralis* Ehrenberg

Present in one sample in the spring from the ocean side. More common in oceanic waters, this species is also found in coastal temperate areas. Reported from the Caribbean by Bucanan (1971), Hargraves et al. (1970), Mar-

shall (1973), and Takano (1960). Reference: Hustedt (1927-1930).

#### *Coscinodiscus concinniformis* Simonsen

Occasionally seen in ocean-side samples in both spring and winter. This species was established by Simonsen (1974) and includes in part *C. concinnus* in the sense of Hustedt (1927-1930). The relationship of *C. concinniformis* to *C. concinnus*, *C. concinnooides*, *C. granii*, *C. nobilis* and *C. wailesii* is discussed by Simonsen (1974: 14-16). At least some of the tropical records of *C. concinnus* are probably *C. concinniformis*, since the latter appears to be a tropical species, whereas the former is found in "higher latitudes." Assuming this to be true, *C. concinniformis* is widespread in the Caribbean. Reference: Cupp (1943); Simonsen (1974).

#### *Coscinodiscus jonesianus* (Greville) Ostenfeld (Figure 85e)

Found once in a winter sample from the lagoon side. Widespread in tropical and temperate coastal areas. Previously reported from the Caribbean by Hargraves et al. (1970), Margalef (1968), and Takano (1960). Reference: Hustedt (1927-1930).

#### *Coscinodiscus nitidus* Gregory

A distinctive species occasionally found in lagoon samples in both spring and winter. Commonly a benthic species. A widespread species of coastal regions. Commonly reported throughout the Caribbean region. Reference: Hustedt (1927-1930).

#### *Coscinodiscus rothii* (Ehrenberg) Grunow

Seen rarely in a lagoon sample in winter. A widespread species often seen in waters of reduced salinity. Previously reported from the Caribbean by Hargraves et al. (1970) and Hagelstein (1938). This is a morphologically variable species, and the taxonomy of the group *Fasciculati*, to which this species belongs, is somewhat confused. Reference: Hustedt (1927-1930).

#### *Coscinodiscus* sp.

Rarely seen in winter in lagoon samples, this species has features that resemble both *C. perforatus* Ehrenberg and *C. apiculatus* Ehren-

berg. The former species has been reported several times from the Caribbean, whereas the latter has not.

*Cylindrotheca closterium* (Ehrenberg) Reimann and Lewin

[= *Nitzschia closterium* (Ehrenberg) Smith]

Rare to common in all samples, but more common in samples from shallow water. This species is ubiquitous in the plankton and benthos from boreal to tropical regions. Previously reported from the Caribbean by Margalef (1957) and Hagelstein (1938). Reference: Hendey (1964; as *N. closterium*).

*Eucampia zoodiacus* Ehrenberg

Seen once in a lagoon sample in winter. A widespread coastal temperate species, uncommon in the tropics. Previously reported from the Caribbean by Buchanan (1971) and Sander (1976). Reference: Cupp (1943).

*Guinardia flaccida* (Castracane) Péragallo

Fairly common in winter from both lagoon and ocean-side samples. Widespread and common in coastal and oceanic regions; it is predominantly temperate but also found in tropical areas. Commonly reported in the Caribbean region (for instance, Sander, 1976). Reference: Hustedt (1927–1930).

*Hemiaulus hauckii* Grunow in Van Heurck (Figure 86d)

Found to be fairly common in ocean-side samples in both spring and winter. This species occurs worldwide in tropical waters, occasionally abundant. Commonly reported from the Caribbean (for instance, Hargraves et al., 1970; Sander, 1976). Reference: Hustedt (1927–1930).

*Hemiaulus membranaceus* Cleve

Distribution similar to that of *H. hauckii* in Belize waters. Normally this species is a rare member of tropical plankton. The polymorphism of this species has been discussed by Sournia (1968). Previously recorded from the Caribbean by Hargraves et al. (1970) and Marshall (1973). Reference: Cupp (1943).

*Hemiaulus sinensis* Greville

Found rarely in lagoon samples in spring and

ocean-side samples in winter. A widespread but uncommon species of tropical areas. Previously reported from the Caribbean by several investigators. Reference: Hustedt (1927–1930).

*Isthmia enervis* Ehrenberg (Figure 87e)

Commonly found in most samples, winter and spring. This distinctive species is normally epiphytic on algae and seagrasses in tropical and temperate waters; more common in the tropics. Several investigators have reported it from the Caribbean. Reference: Hustedt (1927–1930).

*Nitzschia bicapitata* Cleve

This species was rarely seen in ocean-side samples in both seasons. It is a widespread oceanic species from polar regions to the tropics. It has previously been reported from the Caribbean by Hargraves et al. (1970). Reference: Hasle (1960).

*Nitzschia marina* Grunow

Found occasionally in ocean-side samples in the spring. A widespread species in tropical waters. Previously reported from the Caribbean by Hargraves et al. (1970). Reference: Simonsen (1974).

*Nitzschia pseudodelicatissima* Hasle

Seen once in a winter sample from the ocean side of Carrie Bow Cay. This species is difficult to distinguish from *N. delicatissima* Cleve in the light microscope. The distribution of this species in tropical waters is highly uncertain. Several authors have reported *N. seriata* in the tropical Atlantic and Caribbean but Hasle (1971) has shown that *N. seriata* does not occur south of 45°N; several other seriate species are morphologically similar. Some of the tropical and Caribbean records are probably *N. pseudodelicatissima* or a closely related species. The only listing positively noted as *N. pseudodelicatissima* is by Buchanan (1971). Reference: Hasle (1971).

*Odontella aurita* (Lyngbye) Agardh

[= *Biddulphia aurita* (Lyngbye) Brebisson]

Present in a sample from the lagoon side in winter. This is a benthic species, often epiphy-

tic but occasionally found in the plankton. It is widespread in temperate coastal waters, less common in the tropics. Previously reported from the Caribbean by Hagelstein (1938) and Sander (1976). The distinction between *Bidulphia* and *Odontella* is reviewed by Simonsen (1974). Reference: Hustedt (1927-1930).

*Odontella mobiliensis* (Bailey) Grunow

[= *Bidulphia mobiliensis* Grunow in Van Heurck]

Occasionally seen in lagoon samples of both seasons. A widespread species characteristic of temperate and tropical coastal plankton. Widely reported from the Caribbean (for instance, Hargraves et al., 1970; Sander, 1976; Margalef, 1968). Reference: Hustedt (1927-1930).

*Odontella sinensis* (Greville) Grunow

[= *Bidulphia sinensis* Greville]

Comments for *O. mobiliensis* apply here as well.

*Paralia sulcata* (Ehrenberg) Cleve

[= *Melosira Sulcata* (Ehrenberg) Kützing]

A widely distributed coastal form, found during winter and spring, apparently equally at home in the plankton and benthos. More common in temperate than tropical areas. Found in the Caribbean by Hagelstein (1938), Marshall (1973), and Buchanan (1971). Reference: Hendey (1964).

\**Pleurosigma chilensis* Krasske

Very rare in an ocean-side sample in spring, this species is rare and its distribution poorly known. It is one of the very few planktonic species of this genus. Not previously reported from the Caribbean, although the *P. pelagicum* reported by Takano (1960) could be this species. Reference: Krasske (1941).

*Rhizosolenia acuminata* (Péragallo) Gran

Found rarely in spring in samples from the ocean side of Carrie Bow Cay. An oceanic species commonly found in tropical waters. Reported previously by several investigators from the Caribbean (Sander, 1976; Takano, 1960). Reference: Hustedt (1927-1930).

*Rhizosolenia alata* Brightwell

Occasional in samples from the ocean side in spring. A widespread and often abundant spe-

cies from temperate and tropical coastal waters. This species occurs in several morphological forms, of which the form *indica* (Péragallo) Ostenfeld was also occasionally seen. Often observed in the Caribbean (Hargraves et al., 1970; Marshall, 1973; and others). Reference: Hustedt (1927-1930).

*Rhizosolenia calcaravis* Schultze (Figure 87c)

Common in all samples from both seasons. This species is nominally an oceanic one, but it is also in coastal tropical waters. Widespread and occasionally abundant throughout the Caribbean. Reference: Hustedt (1927-1930).

*Rhizosolenia castracanei* Péragallo

Found once in an ocean-side sample in winter. Nearly always found in tropical waters. Previously reported from the Caribbean by Hargraves et al. (1970), Margalef (1968), and Marshall (1973). Reference: Hustedt (1927-1930).

*Rhizosolenia delicatula* Cleve

Seen once in a winter sample from the ocean side. This species is usually found in boreal or temperate coastal waters. Since it seems to differ from *R. stolterfothii* mainly in the range of cell diameter, number of chloroplasts, and degree of bending of the cell chains, this record may be merely a narrow specimen of *R. stolterfothii* with a minimum bending of the chain. *Rhizosolenia delicatula* has been reported from the Caribbean by Margalef (1968) and Takano (1960). Reference: Hustedt (1927-1930).

*Rhizosolenia hebetata* Bailey forma *semispina* (Hensen) Gran

Rarely seen in a winter sample from the ocean side. An oceanic species common to temperate and tropical waters. In north temperate waters the spine is much reduced and the taxon is called *R. hebetata* forma *hiemalis* Gran. Widely distributed in the Caribbean (Marshall, 1973, and others). Reference: Hustedt (1927-1930).

*Rhizosolenia imbricata* Brightwell

Found once in a winter sample from the ocean side. Widely distributed in tropical and temperate oceanic and coastal waters. Several authors differentiate *R. shrubsolei* from this

species, based on the former's narrower diameter and occurrence in cooler waters, but probably they should not be separated. Widespread throughout the Caribbean. The variety *shrubsolei* has been reported by Hagelstein (1938) and Takano (1960). Reference: Hustedt (1927-1930).

*Rhizosolenia robusta* Norman

Occasionally seen in ocean-side samples in winter. This species is found in oceanic and coastal waters from tropical and occasionally from temperate areas. Previously found in the Caribbean by Hargraves et al. (1970), Margalef (1968), and Takano (1960). Reference: Hustedt (1927-1930).

*Rhizosolenia stolterfothii* Péragallo

Rare in winter samples from the ocean side of Carrie Bow Cay. See comments for *R. delicatula*. Widespread in the Caribbean (for instance, Hargraves et al., 1970; Sander, 1976). Reference: Hustedt (1927-1930).

*Rhizosolenia styliformis* Brightwell

Found in both winter and spring in samples from the ocean side. Widely distributed in coastal and oceanic areas of tropical and temperate waters. Widespread in the Caribbean (Hargraves et al., 1970; Sander, 1976; among others). Reference: Hustedt (1927-1930).

*Skeletonema costatum* (Greville) Cleve

Rare in winter samples. Widespread throughout the world's oceans. Many authors separate this species from *S. tropicum* Cleve on the basis of multiple chloroplasts in the latter. The Belize specimens all had two chloroplasts so that they are unquestionably *S. costatum*. Widely reported from the Caribbean, often perhaps as *S. tropicum*. Reference: Cupp (1943).

*Stephanopyxis palmeriana* (Greville) Grunow

Seen once in a lagoon sample in winter. This is a coastal species common to tropics, occasionally ranging into temperate waters. Previously reported from the Caribbean by Margalef (1968) and Takano (1960). Reference: Cupp (1943).

*Thalassionema nitzschiooides* Grunow (Figure 85f)

Rare in winter samples from both the lagoon

and ocean sides. Widespread in oceanic and coastal areas in temperate and tropical waters, and common in the Caribbean. Reference: Cupp (1943).

\**Thalassiosira eccentrica* (Ehrenberg) Cleve

[= *Coscinodiscus excentricus* Ehrenberg]

Uncommon but usually present in all samples in both spring and winter. A widely distributed tropical and temperate species in both coastal and oceanic waters. Several other species resemble *T. eccentrica* closely and electron microscopy is often useful in differentiating similar species. Found throughout the Caribbean, and often listed as *C. excentricus*; the possibility of occasional misidentifications cannot be excluded. Reference: Cupp (1943; as *C. excentricus*).

\**Thalassiosira lineata* Jouse

Seen once in a spring sample from the ocean side. Apparently widely distributed in warmer waters. This species resembles *T. leptopus* (Grunow) Hasle and Fryxell, and electron microscopy is often necessary to distinguish the two. Not previously reported from the Caribbean, although several researchers report *Coscinodiscus lineatus* Ehrenberg, which is synonymous with *T. leptopus*. Reference: Hasle and Fryxell (1977).

*Thalassiothrix frauenfeldii* Grunow

Seen occasionally in ocean-side samples in winter. A widely distributed oceanic and coastal species in tropical and temperate waters. Several investigators have previously found it in the Caribbean (for example, Sanders, 1976). Reference: Cupp (1943).

\**Thalassiothrix vanhoeffenii* Heiden

Found rarely in ocean-side samples in spring and winter. A tropical oceanic species, *T. vanhoeffenii* is similar to *T. longissima* Cleve and Grunow from which it differs in the lack of marginal spines. Not previously reported from the Caribbean, although Hagelstein (1938) and Margalef (1968) list *T. longissima*. Reference: Simonsen (1974).

\**Triceratium antediluvianum* (Ehrenberg) Grunow

Occasionally present in winter samples from the lagoon side. This is a coastal species in

temperate and tropical waters. Both quadra- and pentavalves were seen. Not previously reported from the Caribbean, but has been seen in the Gulf of Mexico (pers. obs.). Reference: Hustedt (1927-1930).

*Triceratium pentacrinus* (Ehrenberg) Wallach (Figure 87d)

[= *Triceratium balearicum* Cleve and Grunow] Seen once in a lagoon sample in spring. Widely distributed in benthic and coastal samples in tropical waters. Previously reported from the Caribbean by Hagelstein (1938; as *Biddulphia pentacrinus*). Reference: Hustedt (1927-1930; as *T. balearicum*); Simonsen (1974).

*Triceratium shadboltianum* Greville

Found in most samples (although uncommon) in spring and winter. The cells generally resemble the variety of *elongata* Grunow, which, considering species variability of this genus, is of questionable taxonomic status. The species is benthic or planktonic in tropical coastal waters. It has been reported previously from the Caribbean by Hagelstein (1938; as *Biddulphia orbiculata* (Shadbolt) Boy), Hargraves et al. (1970), and Margalef (1968).

*Trigonium formosum* (Brightwell) Hendey (Figure 87b)

[= *Triceratium formosum* Brightwell] Occasionally found in samples of both seasons from the lagoon side of Carrie Bow Cay. Three-, four-, and five-sided valves were seen, all of which, according to some authors, have distinct taxonomic status. This species is primarily benthic, occasionally planktonic, in tropical coastal waters. Hargraves et al. (1970) have previously reported it from the Caribbean. Reference: Hustedt (1927-1930).

## Discussion

Seventy-three diatom taxa were identified in this study. For most species the observed morphological variation might justify further differentiation of varieties and forms, but recent studies of diatoms in culture (Hargraves and Guillard, 1974, among others) have demonstrated a broad

morphological plasticity, which makes many names in the literature open to question. This problem will remain unresolved until more species are cultivated and examined. To date, few tropical species have been cultivated.

The most diverse genus is *Chaetoceros* (16 species), followed by *Rhizosolenia* (10 species) and *Coscinodiscus* (7 species). The dominance of representatives of these genera in tropical waters has been noted before; Takano (1960), and Roukiyainen et al. (1973) list 42, 14, and 16 species for these genera, respectively, from the Caribbean. These are impressive numbers, even allowing for misidentifications. In the material studied for this report, several additional species of *Chaetoceros*, *Coscinodiscus*, and *Bacteriastrum* were noted which could not be identified with certainty.

A valuable characteristic in the identification of plankton diatoms is the presence of resting spores, particularly within the genus *Chaetoceros*. For unknown reasons spores are rare in tropical waters. No spores were seen among the species listed here, although at least seven form spores in temperate waters. Margalef (1968) illustrates several species with resting spores but fails to indicate whether they were, in fact, observed in his samples. Likewise, Takano (1960) shows resting spores in *C. affine*, but indicates that the material used as an illustration came from Aomori Bay, Japan. Species of *Bacteriastrum*, *Cerataulina*, *Rhizosolenia*, *Stephanopyxis*, and *Thalassiosira* are also known to form spores, but none were seen. The almost total lack of resting spores in species presumably capable of spore formation presents a problem for those interested in speciation and biogeographical ecology of phytoplankton.

It is often assumed that extensive season fluctuations of phytoplankton do not occur in tropical waters as compared to temperate regions (Parsons et al., 1977). Near Carrie Bow Cay 26 species of diatoms were found in spring and winter, 27 species only in winter, and 20 species only in spring samples. That is, 64% of the species listed here appear to be seasonal in occurrence. Most data on annual cycles of tropical phytoplankton, however, are based on measurements of chlorophyll or isotopic carbon uptake and not species

succession. Thus, what appears to be a contradiction may not be. Tropical waters could have an intricate species succession pattern and yet relatively minor fluctuations in annual production rates. It is perhaps premature to attach major

significance to these samples, which were collected during two seasons. Clearly needed is a complete analysis of the annual cycle of species succession and diversity coupled with primary productivity measurements.

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# Marine Algae and Seagrasses from Carrie Bow Cay, Belize

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and Katina E. Bucher

## ABSTRACT

A total of 165 taxa of benthic marine algae and three of seagrasses (angiosperms) has been found in the intertidal and subtidal habitats of Carrie Bow Cay, South Water Cay, and Twin Cays on the central barrier reef, Belize. Of the algae, 52 are Chlorophyta, 23 Phaeophyta, and 90 Rhodophyta; 34 genera, 77 species, six varieties and five forms represent new records for Belize. The annotated list includes for each taxon the date, page and place of valid publication of its name, selected references to descriptions and illustrations, collecting stations with notes on habitats, and records of distribution within the Caribbean. The nomenclature, morphology, and taxonomy of several species are critically reviewed.

## Introduction

Despite the diverse marine habitats of the mainland coast, barrier reef, atolls, and numerous cays of Belize, Central America, little has been recorded about its marine plants. To date, only two floristic lists have dealt with the marine algae of Belize, the first of which included algal collections of C. L. Lundell and W. C. Schipp (Taylor, 1935). Eighty-four marine algal species included in this paper were later incorporated into Taylor's comprehensive book on algae of the eastern tropical and subtropical coasts of the Americas (1960).

Recently, Tsuda and Dawes (1974) published a list of marine plants collected at Glover's Reef Belize. In their treatment of *Polysiphonia* from Carrie Bow Cay, Kapraun and Norris (herein: 225) report seven taxa new to Belize. Seagrasses were reported in Belize by den Hartog (1970). These studies brought the number of benthic algae and seagrasses recorded from Belize to 159 taxa.

**ACKNOWLEDGMENTS.**—We are grateful to I. A. Abbot for studying the *Helminthocladiaeae* and *Antithamnion*, D. Cheney for examination and discussion of *Eucheuma echinocarpum* and *E. schrammii*, S. Earle for the list of species she found at Carrie Bow Cay (April 1974), and W. Adey and J. L. Connor for discussion on tropical algal species. W. Fenical, O. McConnell, I. Macintyre, F. R. Fosberg, M. Dante, B. Spracklin, T. Rath, W. Gerwick, and A. Cohen assisted as diving partners and shared their algal collections. Our thanks to S. Rechen and R. Sims for processing some of the specimens, and especially to C. Feller for the illustrations of algae. A. R. Tangerini skillfully prepared the maps and M. E. Hale printed their legends. In particular, we thank I. A. Abbott, C. J. Dawes, and R. B. Searles for reading the manuscript and their helpful comments, and D. H. Nicolson for critically reading and discussing our remarks on nomenclature.

## Study Area and Methods

During three ten-day expeditions to the Belizean barrier reef in the spring (March–May) of

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1976, 1977, and 1979, benthic marine algae and seagrasses were collected in the vicinity of Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ), and nearby South Water and Twin cays (Figures 88, 89). This area and the characteristics of its habitats are discussed by Rützler and Macintyre (herein: 9).

In the following presentation higher taxa are arranged phylogenetically, species alphabetically. Taxa reported for the first time in Belize are marked with an asterisk. The author, date, and page of publication of the name of each taxon are given, and wherever possible the original source was examined by us. In place of a typical synon-

ymy we include one or more references to published descriptions and illustrations suitable for identification in the hope of facilitating and encouraging further studies on the algae of Belize. Each collecting locality (field station) is numbered and shown on the maps (Figures 88b, 89). Habitat data of each collecting locality are listed below. For Caribbean distribution, we include published records, from references presently known to us, on the Central American coast from Mexico's Yucatan Peninsula to Venezuela, the Greater and Lesser Antilles, and the Bahama Islands. Specimens were collected by the authors

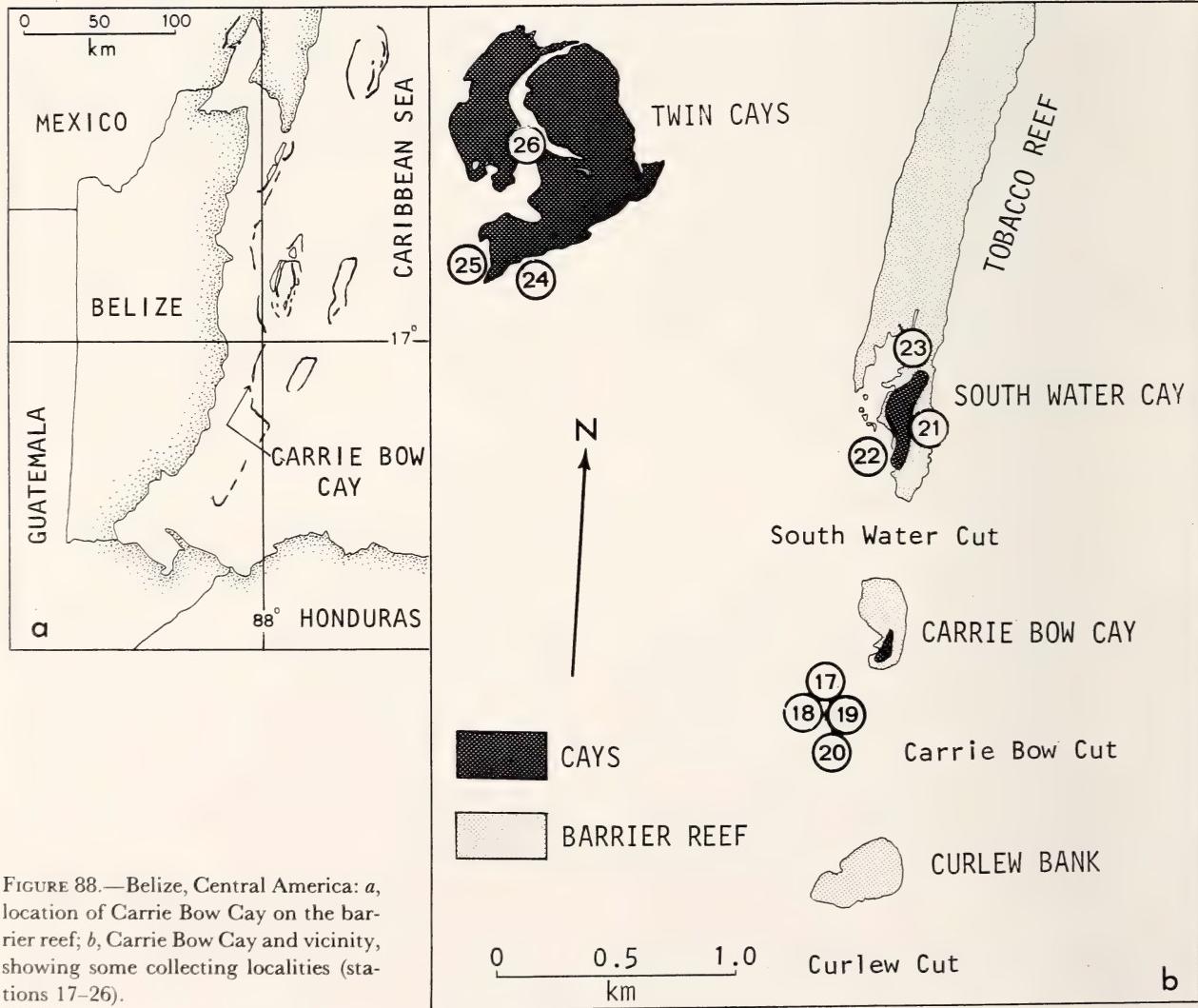


FIGURE 88.—Belize, Central America: *a*, location of Carrie Bow Cay on the barrier reef; *b*, Carrie Bow Cay and vicinity, showing some collecting localities (stations 17–26).

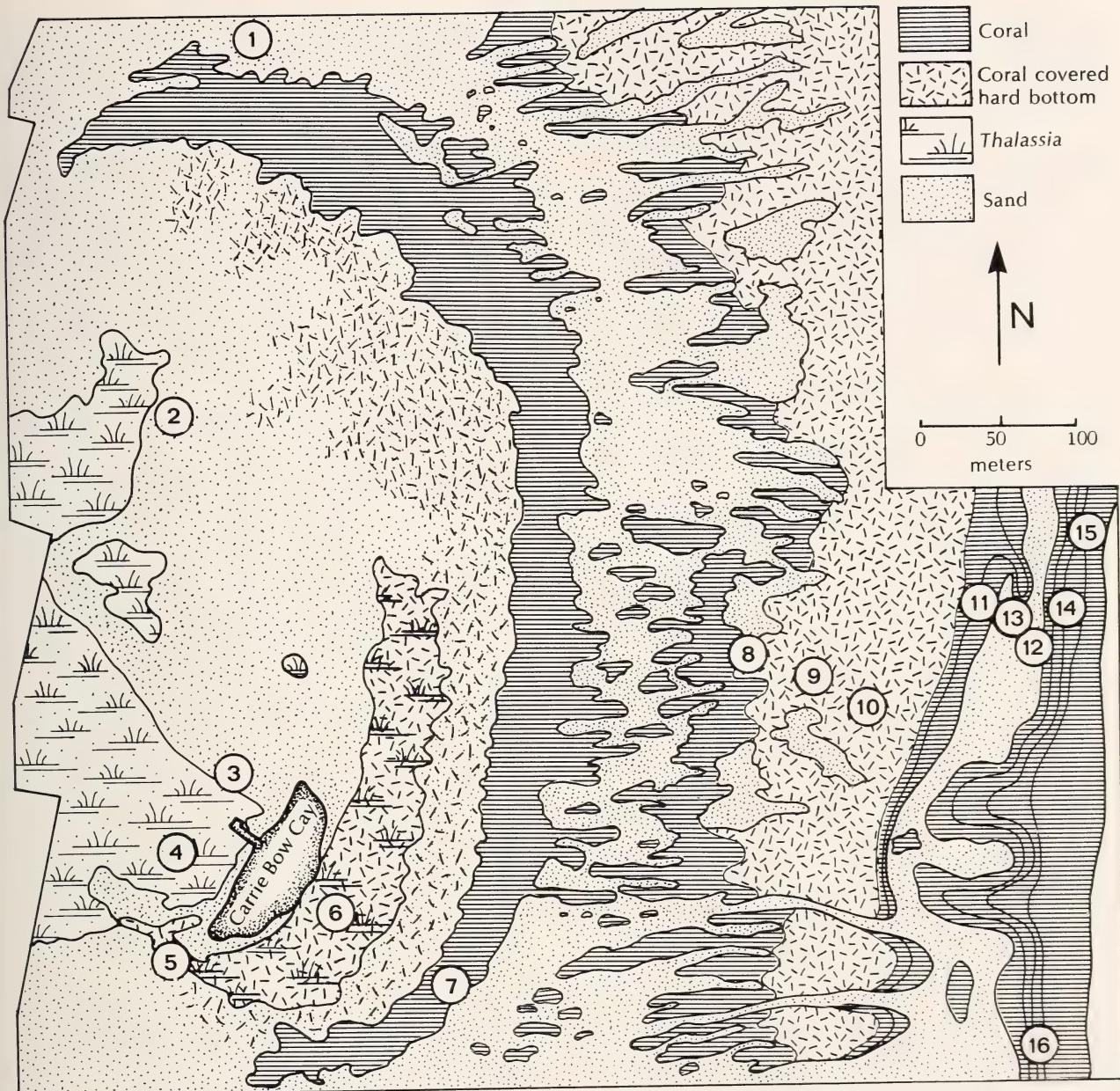


FIGURE 89.—Habitats and simplified substrate types in the vicinity of Carrie Bow Cay, with some collecting localities (stations 1–16).

unless otherwise noted; the numbers with prefix JN refer to the authors' field notebooks. Symbols for reproductive condition are as follows: bisporangia ( $\ominus$ ); cruciate or tetrahedral tetrasporangia ( $\oplus$ ); zonate tetrasporangia ( $Z$ ); carposporangia or cystocarps ( $\ominus$ ); spermatangia ( $\delta$ ); and mono-

cious thallus ( $\varnothing$ ). Material studied will be deposited in the United States National Herbarium, Smithsonian Institution (US), with duplicates sent to the herbaria of the University of California, Berkeley (UC), the University of Michigan (MICH), and to the Fisheries Unit, Belize City.

## Station List

(With habitat and depth data; station numbers keyed to Figures 88b, 89)

### CARRIE BOW CAY

1. South Water Cut, along south side of channel between South Water and Carrie Bow cays; on sands, pavement rock, and coral rubble, and among corals and gorgonians, 3–9 m.
2. North of cay, near 0 m to 100 m section of IMSWE transect; sand and coral rubble, 2–3 m.
3. West of cay, protected shallows of inner lagoon; sand, 1.5 m.
4. West of cay, in *Thalassia* bed; sand and coral rubble, 2–5 m.
5. South of cay, on reef; among corals and gorgonians, 2–5 m.
6. East of cay, reef flat on lee side of reef crest; coral and rubble-covered hard bottom, intertidal to 1 m.
7. East of cay, on reef crest; coral rubble and rock, intertidal to 1 m.
8. Northeast of cay, high-relief spur and groove zone, coral and sand-filled channels, 4.5–6.5 m.
9. Northeast of cay, area between high- and low-relief spur and groove zones, corals, 7.5–9.0 m.
10. Northeast of cay, low-relief spur and groove zone, corals, 9–12 m.
11. Northeast of cay, inner trough, vicinity of IMSWE transect; corals, 12.0–13.5 m.
12. Northeast of cay, sand trough on lee side of outer reef; sand and coral rubble, 18–20 m.
13. Northeast of cay, outer trough and slope of reef; corals and coral rubble, some sand, 18–23 m.
14. Northeast of cay, outer ridge of reef; coral rubble, 15 m.
15. Northeast of cay, fore-reef slope, vicinity of IMSWE transect; corals, 18–40 m.
16. Southeast of cay, outer ridge of reef; corals, 15–30 m.

### PATCH REEFS AND *Thalassia* BEDS, SOUTH OF CARRIE BOW CAY

17. Southwest of cay, coral patch reef; 6.5–8.0 m.
18. Southwest of cay, coral patch reef; 7.5 m.

19. Southwest of cay, coral patch reef; 7.5–9.0 m.
20. Southwest of cay, in *Thalassia* bed; sand, 6.5–7.5 m.

### SOUTH WATER CAY

21. East of cay, inside of reef crest; coral-covered hard bottom, 0.5–1.0 m.
22. West of cay, sheltered sand-bottom lagoon; on rocks, coral rubble and wood pier pilings, 0.5–1.0 m.
23. North of cay, lee side of reef crest; sand and coral rubble, 1–2 m.

### TWIN CAYS

24. East cay of Twin Cays, among mangroves; roots of *Rhizophora mangle* Linnaeus (red mangrove) and sediments held by the roots. Intertidal to 1 m.
25. Southeast end of east cay of Twin Cays; sand and coral rubble bottom, intertidal to 1.0 m.
26. West cay of Twin Cays, channel between Cays; mangrove roots, and sand among *Thalassia*, intertidal to 2 m.

## Division CHLOROPHYTA

### Order CHAETOPHORALES

#### Family CHAETOPHORACEAE

##### \* *Entocladia vagans* (Børgesen) Taylor

*Entocladia vagans* (Børgesen) Taylor, 1960:49.—Børgesen, 1920:418, fig. 400 [as *Endoderma vagans*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, growing within the cell walls of *Griffithsia globulifera*, 22 Apr 1977, JN-6991b.

CARIBBEAN DISTRIBUTION.—Virgin Islands (Børgesen, 1920).

REMARKS.—This minute epiphyte, representing a genus new to Belize, was found within the same host from which it was originally described (Børgesen, 1920).

##### \* *Ulvella lens* P. and H. Crouan

*Ulvella lens* P. and H. Crouan, 1859:288.—Taylor, 1960:52, pl. 2: fig. 7.

LOCAL DISTRIBUTION.—Carrie Bow Cay; sta 7, epiphytic on *Cladophoropsis membranacea*, 22 Apr

1977, JN-6949b.

CARIBBEAN DISTRIBUTION.—Virgin Islands (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—Another microscopic epiphyte that is a new Belizean record for the genus.

### Order ULVALES

#### Family ULVACEAE

##### \**Enteromorpha chaetomorphoides* Børgesen

*Enteromorpha chaetomorphoides* Børgesen, 1911:149; 1913:5, fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 10, epiphytic on *Stylopodium zonale*, 23 Apr 1977, JN-6924 (fertile).

CARIBBEAN DISTRIBUTION.—Jamaica, Puerto Rico, Virgin Islands, Barbados (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Dominican Republic (Almodóvar and Bonnelly, 1977); Costa Rica (Dawson, 1962b); Curaçao (Diaz-Piferrer, 1964b); Trinidad (Richardson, 1975); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—Our specimen is in general agreement with *Enteromorpha chaetomorphoides* as described by Børgesen (1911, 1913) and Taylor (1960); with cells mostly 16–18 µm diameter, with slightly larger and sometimes elongate cells (to 40 µm long) in the broader portions of the thallus.

##### \**Enteromorpha clathrata* var. *crinita* (Roth) Hauck

*Enteromorpha clathrata* var. *crinita* (Roth) Hauck, 1884:429.—Scagel, 1966:48, pl. 25: figs. A–E [as *Enteromorpha crinita*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-7127.

CARIBBEAN DISTRIBUTION.—Cuba, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Grenada (Taylor, 1960); Nevis, Dominica (Taylor, 1969); Isla San Andrés (Kapraun, 1972); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—The above distribution is of records for the species, *Enteromorpha clathrata*. These should be re-examined as some may possibly be var. *crinita*. The Carrie Bow Cay specimen super-

ficially resembles *E. chaetomorphoides* but has cells much larger throughout the thallus, 18–30 µm wide and (18-) 30–45 µm long, and thus is closer to *E. clathrata* var. *crinita* (see Norris, 1976:73–74).

##### \**Enteromorpha flexuosa* (Wulfen ex Roth)

J. Agardh

*Enteromorpha flexuosa* (Wulfen ex Roth) J. Agardh, 1883: 126.—Bliding, 1963:73–79, figs. 38–40.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, 31 Mar 1976, JN-6287.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Barbuda, Guadeloupe, Barbados, Grenada, Costa Rica, Netherlands Antilles, Venezuela, Tobago (Taylor, 1960); St. Kitts, Antigua, Montserrat, Dominica, St. Vincent, Bequia (Taylor, 1969); Isla San Andrés (Kapraun, 1972); Trinidad (Richardson, 1975).

REMARKS.—This species is widespread in the Pacific and Atlantic Oceans (see Abbot and Hollenberg, 1976; Bliding, 1963).

##### \**Ulva rigida* C. Agardh

*Ulva rigida* C. Agardh, 1823:410.—Bliding, 1968:546, figs. 6A–E, 7A–F, 8A–E, 9A–I, and 10A–B.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, 31 Mar 1976, JN-6285a,b.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Martinique, St. Vincent, Barbados, Grenada, Costa Rica, Panama, Colombia, Venezuela, Trinidad (Taylor, 1960, as *U. lactuca* var. *rigida*); Grand Cayman, Antigua, Dominica (Taylor, 1969, as “var. *lactuca* or near var. *rigida*”).

REMARKS.—The Twin Cays specimens possess the microscopic dentation along the blade margins, characteristic of this species (Bliding, 1968).

### Order CLADOPHORALES

#### Family CLADOPHORACEAE

##### *Cladophora* cf. *fuliginosa* Kützing

*Cladophora fuliginosa* Kützing, 1849:415.—Taylor, 1960:83, pl. 2: fig. 3, pl. 3: fig. 4.

LOCAL DISTRIBUTION.—South Water Cay: sta 23, 30 Apr 1979, JN-7329.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Turks Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Belize, Netherlands Antilles (Taylor, 1960); Nevis, Antigua, Dominica, St. Lucia (Taylor, 1969).

REMARKS.—Our material resembles this taxon, but differs in cell size. The cells of the axes and branches are much larger and of similar diameter throughout, mostly 590  $\mu\text{m}$  diameter and (2-) 3-4 times as long; upper cells of the branches were 580  $\mu\text{m}$  diameter, slightly tapered towards apices, and up to 12 times as long. These measurements are almost 1.6 times the diameter reported for *Cladophora fuliginosa* (Taylor, 1960), which has main axes cells to 380  $\mu\text{m}$  diameter and 3-6 times as long, with branch cells 150-160 (-290)  $\mu\text{m}$  diameter and 10-13 times as long as wide.

We are aware that the earliest available name for this taxon is *Cladophora catenata* (Linnaeus) Kützing, 1843 (van den Hoek, 1963:123). However, the name “*C. catenata* (C. Agardh) Ardisson in Rabenhorst” is widely used in a different taxonomic sense (see for instance, Collins, 1909:347; Taylor, 1960:83), and does not include the actual Linnaean type. Thus, it seems, *C. catenata* may be a good candidate for rejection under Article 69 (Stafleu et al., 1978), an action we are considering.

#### Order SIPHONOCLADIALES

#### Family SIPHONOCLADACEAE

##### \**Cladophoropsis macromeres* Taylor

*Cladophoropsis macromeres* Taylor, 1928:64; 1960:118, pl. 2: fig. 2.

LOCAL DISTRIBUTION.—Twin Cays: sta 25, epiphytic on *Digenia simplex*, 26 Apr 1977, JN-6894a.

CARIBBEAN DISTRIBUTION.—Cuba (Sosa, 1977); Puerto Rico (Diaz-Piferrer, 1963); Jamaica (Taylor, 1960; Chapman, 1961); Barbados (Taylor, 1969).

#### *Cladophoropsis membranacea* (C. Agardh) Børgeesen

*Cladophoropsis membranacea* (C. Agardh) Børgeesen, 1905:275.—Taylor, 1960:117, pl. 2: fig. 1, pl. 3: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6949a.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Barbados, Grenada, Belize, Panama, Netherlands Antilles, Venezuela, Tobago (Taylor, 1960); Grand Cayman, St. Kitts, Antigua, Dominica, St. Lucia, St. Vincent, Bequia (Taylor, 1969); Costa Rica (Dawson, 1962b); Panama (Earle, 1972); Isla San Andrés (Kapraun, 1972).

#### Family VALONIACEAE

##### *Dictyosphaeria cavernosa* (Forsskål) Børgeesen

*Dictyosphaeria cavernosa* (Forsskål) Børgeesen, 1932:2.—Taylor, 1960:116, pl. 7: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6401; sta 7, 21 Apr 1977, JN-6977; sta 10, 23 Apr 1977, JN-6915; sta 14, 27 Apr 1977, JN-6797; sta 18, 25 Apr 1977, JN-6741. South Water Cay: sta 21, 28 Apr 1977, JN-6715; sta 23, 30 Apr 1979, JN-7328. Twin Cays: sta 25, 26 Apr 1977, JN-6862.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Turks Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Nevis, Guadeloupe, Martinique, Barbados, Netherlands Antilles, Panama, Isla las Aves (Taylor, 1960); Antigua, Dominica, St. Lucia, Bequia, Grenada (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b).

##### \**Valonia macrophysa* Kützing

*Valonia macrophysa* Kützing, 1843:307.—Taylor, 1960:110, pl. 2: fig. 6, pl. 7: fig. 4.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 27 Apr 1977, JN-6405; sta 9, 29 Apr 1977, JN-6819b.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands (Taylor, 1960); Nevis, Antigua, Barbados, St. Vincent, Bequia (Taylor, 1969); Puerto Rico (Diaz-Piferrer, 1963); Curaçao (van den Hoek, 1969); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—*Valonia macrophysa* is often covered with small epiphytic filamentous and thin crustose coralline red algae.

### **Valonia ventricosa J. Agardh**

*Valonia ventricosa* J. Agardh, 1885:96.—Taylor, 1960:110, pl. 9: figs. 4, 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 30 Mar 1976, JN-7257; sta 7, 22 Apr 1977, JN-6963; sta 9, 27 Apr 1977, JN-6406; sta 14, 17 Apr 1977, JN-6798. South Water Cay: sta 23, 30 Apr 1979, JN-7318. Twin Cays: sta 25, 26 Apr 1977, JN-6864; sta 26, 29 Apr 1979, JN-7296.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Grenadines, Grenada, Old Providence Island, Panama, Netherlands Antilles, Tobago (Taylor, 1960); St. Kitts, Nevis, Antigua, St. Lucia, St. Vincent, Bequia (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b).

### **Family BOODLEACEAE**

#### ***Struvea anastomosans* (Harvey) Piccone and Grunow ex Piccone**

*Struvea anastomosans* (Harvey) Piccone and Grunow ex Piccone, 1884:20.—Børgesen, 1913:54, fig. 39a-f.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7492.

CARIBBEAN DISTRIBUTION.—Jamaica, Virgin Islands, Guadeloupe, Barbados, Venezuela, Trinidad, Tobago (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Puerto Rico (Almodóvar and Blomquist, 1965); Dominica (Taylor, 1969); Costa Rica (Dawson, 1962b); Belize (Tsuda and Dawes, 1974); Curaçao, Bonaire (Diaz-Piferrer, 1964b).

### **Family ANADYOMENACEAE**

#### ***Anadyomene stellata* (Wulfen) C. Agardh**

*Anadyomene stellata* (Wulfen) C. Agardh, 1823:400.—Taylor, 1960:125, pl. 7: fig. 2, pl. 8: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 9, 29 Apr 1977, JN-6819a; sta 10, 23 Apr 1977, JN-6921; sta 14, 27 Apr 1977, JN-6799. Twin Cays: sta 24, on mangrove roots, 31 Mar 1976, JN-6282 and JN-6294; sta 25, 26 Apr 1977, JN-6865; sta 26, 22 Apr 1979, JN-7446.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Belize, Panama (Taylor, 1960); Nevis, Antigua, Dominica, St. Lucia (Taylor, 1969); Costa Rica (Dawson, 1962b); Venezuela (Diaz-Piferrer, 1970b); Curaçao (Diaz-Piferrer, 1964b).

#### **\**Microdictyon boergesenii* Setchell**

*Microdictyon boergesenii* Setchell, 1925:106.—Taylor, 1960:120, pl. 8: fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 15, 27 Apr 1977, JN-6685.

CARIBBEAN DISTRIBUTION.—Cuba (Sosa, 1977); Jamaica, Guadeloupe, Virgin Islands (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Barbados (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b).

REMARKS.—Reported from moderately deep water, this species (a new Belizean record of the genus) was found at 22 m depth in Belize.

#### **\**Valoniopsis pachynema* (Martens) Børgesen**

*Valoniopsis pachynema* (Martens) Børgesen, 1934a:10, figs. 1-2.

LOCAL DISTRIBUTION.—South Water Cay: sta 23, 30 Apr 1979, JN-7326 (fertile?).

CARIBBEAN DISTRIBUTION.—Cuba (Suarez, 1973); Hispaniola (Taylor, 1960).

REMARKS.—This is a new record of the genus in Belize.

## Order DASYCLADALES

### Family ACETABULARIACEAE

#### *Acetabularia crenulata* Lamouroux

*Acetabularia crenulata* Lamouroux, 1816:249.—Taylor, 1960: 105, pl. 4: fig. 5, pl. 6: fig. 12.

LOCAL DISTRIBUTION.—Twin Cay: sta 26, on mangrove roots, 29 Apr 1979, JN-7303.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Martin, Guadeloupe, Barbados, Colombia, Netherlands Antilles, Venezuela (Taylor, 1960); Grand Cayman (Taylor, 1969); Panama (Earle, 1972).

#### \* *Acetabularia myriospora* Joly and Cordeiro-Marino

FIGURE 90

*Acetabularia myriospora* Joly and Cordeiro-Marino in Joly et al., 1965:80.—Howe, 1909:92, pl. 6: fig. 21, pl. 8: fig. 10 [as *Acetabulum polyphysoides* f. *deltoidium*].—Taylor, 1960: 105 [as *Acetabularia polyphysoides* f. *deltoidium*].—Valet, 1969:623, pl. 44: figs. 17–20.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, growing on dead coral, in turf, 21 Apr 1977, JN-7051b.

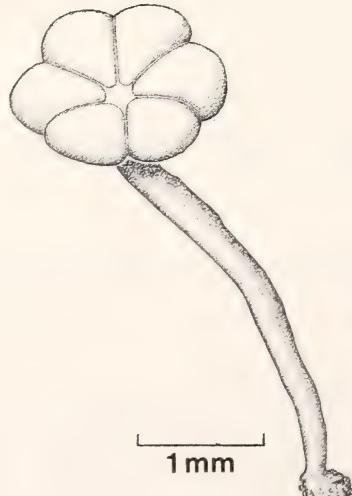


FIGURE 90.—*Acetabularia myriospora*, habit of a thallus (JN-7051b).

CARIBBEAN DISTRIBUTION.—Cuba (Sosa, 1977); Bahamas (Howe, 1909; Valet, 1969).

REMARKS.—Growing on the same coral with the following taxon, *Acetabularia polyphysoides*; it is distinguished by its smaller size, and fewer (5–7), inflated rays. Described from Bahía, Brazil, by Joly and Cordeiro-Marino (Joly et al., 1965); Valet (1969) later considered the earlier described taxon, *Acetabularia polyphysoides* f. *deltoidium* (Howe) Collins (1909), to be a synonym of *Acetabularia myriospora*.

#### \* *Acetabularia polyphysoides* P. and H. Crouan

*Acetabularia polyphysoides* P. and H. Crouan in Schramm and Mazé, 1866:101.—Howe, 1909:92, pl. 6: figs. 16–20, pl. 7: figs. 5–9.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, growing on dead coral, in short turf, 21 Apr 1977, JN-7051a.

CARIBBEAN DISTRIBUTION.—Jamaica, Guadeloupe, Barbados (Taylor, 1960).

REMARKS.—Plants were 2–5 mm tall; 3–4 mm disc diameter, aplanosporangia (55–) 60–75 (–79) in a ray, 86–94  $\mu\text{m}$  diameter; 16–20 rays, heavily calcified between rays; corona superior with 6–10 hairs. The Carrie Bow Cay specimens, though superficially resembling *Acetabularia pusilla* (Howe) Collins, are closer in taxonomic features to *A. polyphysoides*.

### Family DASYCLADACEAE

#### \* *Neomeris annulata* Dickie

FIGURE 91

*Neomeris annulata* Dickie, 1874:198.—Taylor, 1960:101, pl. 5: fig. 5, pl. 6: figs. 4–6.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, on mangrove bark, 26 Apr 1977, JN-6863, and 29 Apr 1979, JN-7398.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Nevis, Guadeloupe, Martinique, Barbados (Taylor, 1960); Cuba (Díaz-Piferrer, 1964a); St. Thomas (Valet, 1969); Antigua, Dominica (Taylor, 1969);

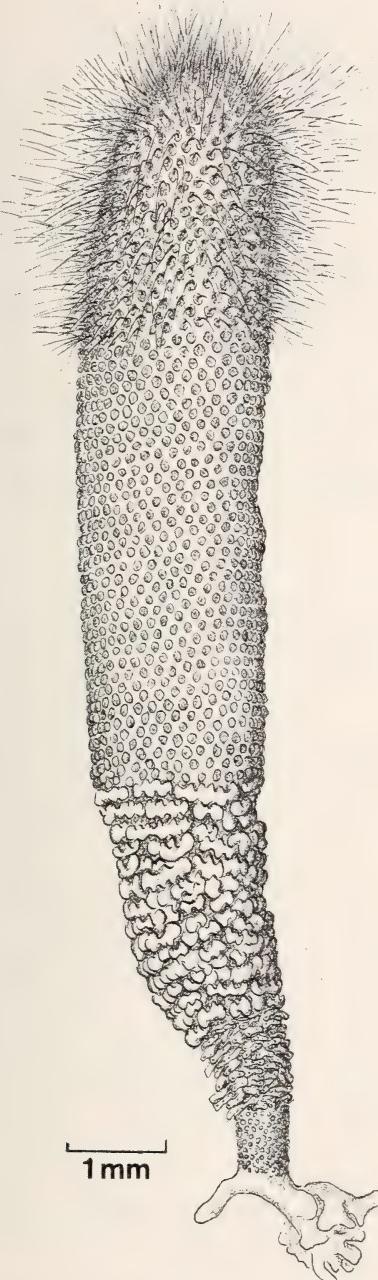


FIGURE 91.—*Neomeris annulata*, habit of a thallus (JN-7398).

Costa Rica (Dawson, 1962b); Panama (Earle, 1972); Curaçao (Diaz-Piferrer, 1964b).

**REMARKS.**—The report of this and the following species constitutes a new record for the genus in Belizean waters.

### \* *Neomeris mucosa* Howe

*Neomeris mucosa* Howe, 1909:84, pl. 5: figs. 1–14.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 21 Apr 1977, JN-6933; sta 7, 22 Apr 1977, JN-6959; sta 9, 29 Apr 1977, JN-6820; sta 10, 23 Apr 1977, JN-6920. South Water Cay: sta 21, 28 Apr 1977, JN-6717.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Netherlands Antilles (Taylor, 1960); Puerto Rico (Almodóvar, 1970); Antigua (Taylor, 1969).

**REMARKS.**—This report represents a new record for this species along the Atlantic coast of Central America. *Neomeris annulata* has calcified sporangia that laterally cohere in regular bands about the thallus. *Neomeris mucosa* differs in having calcified sporangia free and not arranged in bands.

## Order CAULERPALES

### Family CAULERPACEAE

#### \* *Caulerpa ambigua* Okamura

*Caulerpa ambigua* Okamura, 1897:4.—Eubank, 1946:410.—Egerod, 1952:368.—Taylor, 1960:137, pl. 10: figs. 2–9.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, growing with *Bryopsis*, 28 Apr 1979, JN-7414.

**CARIBBEAN DISTRIBUTION.**—Jamaica, Virgin Islands, Barbados, Costa Rica (Taylor, 1960); Antigua, St. Lucia (Taylor, 1969); Cuba (Diaz-Piferrer, 1964a); Puerto Rico (Diaz-Piferrer, 1963); Curaçao (van den Hoek, 1969); Venezuela (Diaz-Piferrer, 1970b).

#### *Caulerpa cupressoides* (Vahl) C. Agardh

*Caulerpa cupressoides* (Vahl) C. Agardh, 1823:441.—Taylor, 1960:146, pl. 14: figs. 3, 4, 6, pl. 15: figs. 1–4, pl. 18: figs. 11–13.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6393; sta 18, 25 Apr 1977, JN-6743. South Water Cay: sta 23, 30 Apr 1979, JN-7334 and JN-7353. Twin Cays: sta 25, 26 Apr 1977, JN-6857.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, St. Eustatius, Guadeloupe, Martinique, St. Vincent, Barbados, Grenada, Belize, Panama, Colombia, Tobago (Taylor, 1960); Grand Cayman, Nevis, Antigua, Dominica (Taylor, 1969); Puerto Rico (Almodóvar, 1964); Costa Rica (Wellington, 1973); Isla San Andrés (Kapraun, 1972); Curaçao (van den Hoek, 1969).

### *Caulerpa fastigiata* Montagne

*Caulerpa fastigiata* Montagne, 1842:19.—Taylor, 1960:136, pl. 10: fig. 12.

LOCAL DISTRIBUTION.—South Water Cay: sta 21, 28 Apr 1977, JN-6729.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Hispaniola, Virgin Islands, Guadeloupe, Barbados, Belize, Panama (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Grand Cayman (Taylor, 1969); Trinidad (Richardson, 1975).

### *Caulerpa mexicana* (Sonder) Kützing

*Caulerpa mexicana* (Sonder) Kützing, 1849:496.—Taylor, 1960:141, pl. 12: figs. 2–5.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, 26 Apr 1977, JN-6860.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Barbados, Belize, Colombia, Venezuela, Tobago (Taylor, 1960); Antigua, Grenada (Taylor, 1969); Costa Rica (Wellington, 1973); Curaçao (Diaz-Piferrer, 1964b; van den Hoek, 1969).

### \* *Caulerpa paspaloides* (Bory) Greville

*Caulerpa paspaloides* (Bory) Greville, 1830:1xiv.—Taylor, 1960:149, pl. 16: figs. 1–4, pl. 18: figs. 8, 14, 15.

LOCAL DISTRIBUTION.—Twin Cays: sta 26, 29 Apr 1979, JN-7285.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cuba, Jamaica (Taylor, 1960).

REMARKS.—This report represents a new record for this species along the Caribbean coast of Central America.

### \* *Caulerpa peltata* Lamouroux

*Caulerpa peltata* Lamouroux, 1809d:145.—Taylor, 1960:155, pl. 17: fig. 2, pl. 18: fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6962.

CARIBBEAN DISTRIBUTION.—Barbuda (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Puerto Rico (Diaz-Piferrer, 1963); Jamaica (Chapman, 1961); Panama (Earle, 1972); Trinidad (Richardson, 1975); Curaçao (Diaz-Piferrer, 1964b).

### *Caulerpa racemosa* (Forsskål) J. Agardh

*Caulerpa racemosa* (Forsskål) J. Agardh, 1873:35.—Taylor, 1960:151, pl. 17: figs. 1, 3, 4, 6, 7, pl. 18: figs. 2–5, 7.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6950, JN-6952, and 21 Apr 1977, JN-6975 and JN-6980. Twin Cays: sta 24, 31 Mar 1976, JN-6288; sta 25, 26 Apr 1977, JN-6858; sta 26, 29 Apr 1979, JN-7282 and JN-7304.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, St. Eustatius, Antigua, Guadeloupe, Martinique, Barbados, Grenadines, Grenada, Belize, Costa Rica, Panama, Colombia, Netherlands Antilles, Isla las Aves, Venezuela, Trinidad, Tobago (Taylor, 1960); Grand Cayman, St. Kitts, Dominica, St. Lucia, St. Vincent, Bequia (Taylor, 1969).

REMARKS.—The most common of the species of *Caulerpa* in the vicinity of Carrie Bow Cay. It is usually abundant where found.

### \* *Caulerpa serrulata* (Forsskål) J. Agardh

FIGURE 92

*Caulerpa serrulata* (Forsskål) J. Agardh, 1823:446.—Børgesen, 1932:5.—Taylor, 1960:145, pl. 14: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 22 Apr 1979, JN-7402; sta 9, 1 May 1979, JN-7518.

CARIBBEAN DISTRIBUTION.—Bahamas, St. Barthélemy, Guadeloupe, Barbados, Grenada, Venezuela (Taylor, 1960).

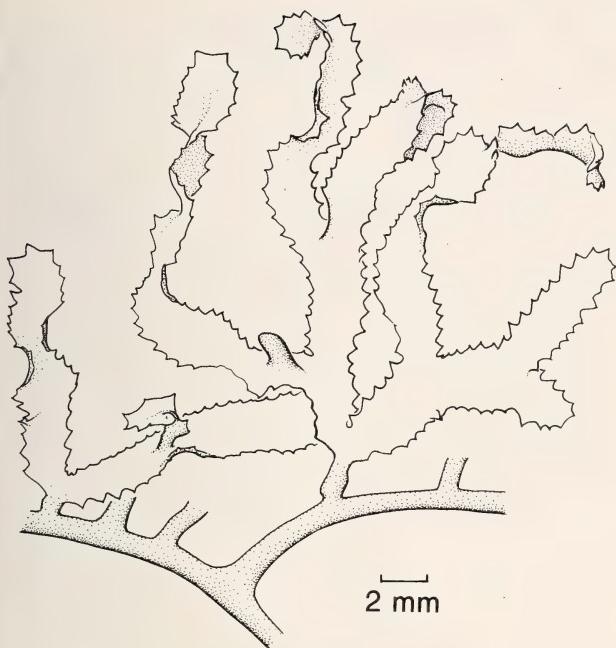


FIGURE 92.—*Caulerpa serrulata*, habit of a portion of the thallus (JN-7402).

### *Caulerpa sertularioides* (Gmelin) Howe

*Caulerpa sertularioides* (Gmelin) Howe, 1905:576.—Taylor, 1960:144, pl. 13: figs. 1–7.

LOCAL DISTRIBUTION.—Twin Cays: sta 25, 26 Apr 1977, JN-6861; sta 26, 29 Apr 1979, JN-7292.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Dominica, Martinique, Barbados, Grenada, Belize, Old Providence Island, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Trinidad, Tobago (Taylor, 1960); Grand Cayman, Antigua, St. Lucia, Bequia (Taylor, 1969); Isla Sán Andrés (Kapraun, 1972).

### \**Caulerpa sertularioides* f. *farlowii* (Weber-van Bosse) Børgesen

*Caulerpa sertularioides* f. *farlowii* (Weber-van Bosse) Børgesen, 1907:365; 1913:133, fig. 106.—Taylor, 1960:144, pl. 13: figs. 4–5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, 23 Apr 1979, JN-7654; sta 7, 21 Apr 1977, JN-6985.

CARIBBEAN DISTRIBUTION.—Virgin Islands (Børgesen, 1907); Aruba Island (Taylor, 1942).

### \**Caulerpa verticillata* J. Agardh

*Caulerpa verticillata* J. Agardh, 1847:6.—Taylor, 1960:138, pl. 10: figs. 1, 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 9, 27 Apr 1977, JN-6412, and 29 Apr 1977, JN-6831; sta 10, 23 Apr 1977, JN-6913, and 25 Apr 1977, JN-6965. Twin Cays: sta 24, 31 Mar 1976, JN-6279; sta 25, 26 Apr 1977, JN-6859; sta 26, 29 Apr 1979, JN-7294.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Antigua, Guadeloupe, Martinique, Grenada, Netherlands Antilles, Venezuela (Taylor, 1960); Grand Cayman (Taylor, 1969); Costa Rica (Dawson, 1962b); Trinidad (Richardson, 1975).

REMARKS.—Though encountered in several habitats, intertidal and subtidal (to 12 m depth), this species was particularly abundant under the mangroves at Twin Cays where it formed extensive green carpets.

## Family BRYOPSIDACEAE

### *Bryopsis pennata* Lamouroux

*Bryopsis pennata* Lamouroux, 1809c:134.—Taylor, 1960:132, pl. 9: fig. 12.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-6984 and JN-7052.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Belize, Colombia, Netherlands Antilles, Trinidad (Taylor, 1960); Antigua (Taylor, 1969).

## Order CODIALES

### Family CODIACEAE

### *Avrainvillea longicaulis* (Kützing) Murray and Boodle

*Avrainvillea longicaulis* (Kützing) Murray and Boodle, 1889: 70.—Taylor, 1960:160, pl. 19: fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 30 Mar 1976, JN-7249.

CARIBBEAN DISTRIBUTION.—Bahamas, Salt Key Bank, Jamaica, Virgin Islands, Antigua, Guadeloupe, Barbados, Grenada, Belize, Isla las Aves (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Grand Cayman (Taylor, 1969); Costa Rica (Dawson, 1962b).

REMARKS.—Our plants had blades composed of cylindrical and torulose filaments similar to *Avrainvillea longicaulis* (Taylor, 1960). However, there is difficulty in distinguishing *A. longicaulis* from *A. nigricans* Decaisne solely on the basis of the morphology of the blade filaments. Chapman (1961) suggests *A. longicaulis* (as “*A. mazei*”) may prove to be a variety of *A. nigricans*. Until more collections and detailed studies have been made on these taxa it seems best to continue to recognize the two as separate species.

There has been some historical confusion in application of the epithet *longicaulis* involving both taxonomy and nomenclature. The basionym, *Rhipilia longicaulis* Kützing (1858:13), pertains to material with a blade composed of torulose filaments. Unfortunately, this epithet was transferred to *Avrainvillea* by Murray and Boodle (1889:70), in the sense of moniliform filaments. Howe (1905:586), on examining portions of the type of *Rhipilia longicaulis* Kützing (Sonder Herbarium, MEL), concluded that it was torulose “the same as the more recently published *A. mazei* [Murray and Boodle, 1889:70]”, and later he (1907:508–510) recognized them as *A. longicaulis*, reducing *A. mazei* to synonymy.

Børgesen (1908), while accepting this taxonomy, rejected the name *Avrainvillea longicaulis* as a nomen confusum and called the taxon *A. mazei*, an opinion more recently followed by Chapman (1961).

Gepp and Gepp (1911:40–42), in reviewing the situation, questioned the identification of the type, *Rhipilia longicaulis* (based on their analysis of Kützing’s published illustration), and suggested it be identified as “*Avrainvillea sordida* Murray and Boodle” [= *A. levis* Howe, 1905] a later homonym of *A. sordida* (Montagne) P. and H. Crouan ex Mazé and Schramm (1878).

We accept the taxonomy and nomenclature used by Howe (1905, 1907), and note that this was also accepted by Taylor (1960) without discussion.

### ***Codium intertextum* Collins and Hervey**

*Codium intertextum* Collins and Hervey, 1917:54.—Silva, 1960: 500, pl. 107: figs. a–e, pl. 108: fig. a.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-6976.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Kitts, Guadeloupe, Barbados, Netherlands Antilles, Venezuela (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b).

## **Family UDOTEACEAE**

### ***Halimeda copiosa* Goreau and Graham**

*Halimeda copiosa* Goreau and Graham, 1967:432–441.—Colinvaux, 1968:30, fig. 1 [as *Halimeda hederacea*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 21 Apr 1977, JN-6930; sta 15, 5 Apr 1976, JN-7650.

CARIBBEAN DISTRIBUTION.—Jamaica, Curaçao (Colinvaux, 1968); Belize (Tsuda and Dawes, 1974); Venezuela (Diaz-Piferrer, 1970b).

### ***Halimeda discoidea* Decaisne**

*Halimeda discoidea* Decaisne, 1842:112.—Taylor, 1960:179, pl. 24: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7010, and 21 Apr 1977, JN-6935; sta 8, 29 Mar 1976, JN-6157a, and 22 Apr 1979, JN-7403; sta 10, 23 Apr 1977, JN-6900; sta 11, 29 Apr 1977, JN-6833; sta 14, 27 Apr 1977, JN-6784, and 1 May 1979, JN-7362; sta 15, 27 Apr 1977, JN-6684; sta 17, 25 Apr 1977, JN-7017.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Panama, Colombia, Venezuela (Taylor, 1960); Antigua, St. Lucia (Taylor, 1969); Belize (Tsuda and Dawes, 1974).

### ***Halimeda goreauii* Taylor**

*Halimeda goreauii* Taylor, 1962a:173, figs. 1-7.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 30 Apr 1979, JN-7345; sta 10, 25 Apr 1977, JN-6966; sta 14, 27 Apr 1977, JN-6792, and 1 May 1979, JN-7363; sta 15, 5 Apr 1976, JN-6333, and 27 Apr 1977, JN-6681.

**CARIBBEAN DISTRIBUTION.**—Cuba (Suarez, 1973); Jamaica (Taylor, 1962a); Puerto Rico (Almodóvar and Blomquist, 1965); Belize (Tsuda and Dawes, 1974).

### ***Halimeda incrassata* (Ellis and Solander) Lamouroux**

*Halimeda incrassata* (Ellis and Solander) Lamouroux, 1812: 186.—Taylor, 1960:181, pl. 23: figs. 1, 4.

**LOCAL DISTRIBUTION.**—South Water Cay: sta 21, 20 Apr 1977, JN-6726. Twin Cays: sta 24, 31 Mar 1976, JN-6281, and 26 Apr 1977, JN-6851, and 29 Apr 1979, JN-7381; sta 26, 29 Apr 1979, JN-7280.

**CARIBBEAN DISTRIBUTION.**—Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Martin, St. Barthélemy, Guadeloupe, Dominica, Martinique, Barbados, Grenada, Belize, Panama, Netherlands Antilles (Taylor, 1960); Grand Cayman (Taylor, 1969); Venezuela (Diaz-Piferrer, 1970b).

### ***Halimeda opuntia* (Linnaeus) Lamouroux**

*Halimeda opuntia* (Linnaeus) Lamouroux, 1812:186.—Taylor, 1960:176, pl. 23: fig. 3, pl. 24: fig. 1.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-6979; sta 14, 27 Apr 1977, JN-6796; sta 15, 27 Apr 1977, JN-6680. Twin Cays: sta 24, 31 Mar 1976, JN-6289; sta 26, 29 Apr 1979, JN-7291 and JN-7299.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Anguila Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Tortola Island, St. Barthélemy, Guadeloupe, Martinique, Barbados, Grenada, Belize, Old Providence Island, Costa Rica, Panama, Colombia, Netherlands Antilles, Isla las Aves, Ven-

ezuela, Trinidad, Tobago (Taylor, 1960); St. Kitts, Nevis, Antigua, St. Lucia, St. Vincent, Bequia (Taylor, 1969); Isla San Andrés (Kapraun, 1972).

### ***Halimeda tuna* (Ellis and Solander) Lamouroux**

*Halimeda tuna* (Ellis and Solander) Lamouroux, 1812:186.—Taylor, 1960:178, pl. 24: fig. 5.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7009; sta 8, 29 Mar 1976, JN-6157b; sta 9, 29 Apr 1977, JN-6832; sta 10, 23 Apr 1977, JN-6906 and JN-6916, and 25 Apr 1977, JN-6969; sta 14, 27 Apr 1977, JN-6785 and JN-6794; sta 18, 25 Apr 1977, JN-6738.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Anguila Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Martin, Saba Bank, Guadeloupe, Barbados, Belize, Panama, Colombia (Taylor, 1960); St. Kitts, Nevis (Taylor, 1969); Costa Rica (Dawson, 1962b); Isla San Andrés (Kapraun, 1972); Venezuela (Diaz-Piferrer, 1970b).

### ***Penicillus capitatus* Lamarck**

*Penicillus capitatus* Lamarck, 1813:299.—Taylor, 1960:171, pl. 21: fig. 2, pl. 25: fig. 4.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6390a. South Water Cay: sta 21, 28 Apr 1977, JN-6727. Twin Cays: sta 25, 28 Apr 1977, JN-6852; sta 26, 29 Apr 1979, JN-7298.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Martin, St. Barthélemy, St. Eustatius, Guadeloupe, Dominica, Martinique, Grenada, Belize, Old Providence Island, Panama, Colombia, Netherlands Antilles, Isla las Aves (Taylor, 1960); St. Kitts, Antigua (Taylor, 1969); Costa Rica (Dawson, 1962b); Isla San Andrés (Kapraun, 1972).

### ***Penicillus dumentosus* (Lamouroux) Blainville**

*Penicillus dumentosus* (Lamouroux) Blainville, 1834:553.—Taylor, 1960:172, pl. 21:fig. 4, pl. 25: fig. 15.

LOCAL DISTRIBUTION.—Twin Cays: sta 26, 29 Apr 1979, JN-7306.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Grenada, Belize, Old Providence Island, Colombia (Taylor, 1960); St. Kitts, Antigua (Taylor, 1969).

### **Penicillus lamourouxii Decaisne**

*Penicillus lamourouxii* Decaisne, 1842:109.—Taylor, 1960:172, pl. 21: fig. 1, pl. 25: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6390b. Twin Cays: sta 24, 31 Mar 1976, JN-6280.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Jamaica, Puerto Rico, Virgin Islands, St. Eustatius, Guadeloupe, Panama (Taylor, 1960); Grand Cayman (Taylor, 1969); Belize (Tsuda and Dawes, 1974).

### **Penicillus pyriformis A. and E. S. Gepp**

*Penicillus pyriformis* Gepp and Gepp, 1905:1.—Taylor, 1960: 170, pl. 21: figs. 3, 5, pl. 25: fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 30 Mar 1976, JN-7254, and 30 Apr 1979, JN-7348; sta 10, 23 Apr 1977, JN-6901, and 25 Apr 1977, JN-6881; sta 14, 27 Apr 1977, JN-6786.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Virgin Islands, St. Eustatius, Guadeloupe, Panama (Taylor, 1960); Puerto Rico (Almodóvar and Blomquist, 1965); Belize (Tsuda and Dawes, 1974); Curaçao (Díaz-Piferrer, 1964b).

### \***Penicillus pyriformis f. explanatus Børgesen**

*Penicillus pyriformis f. explanatus* Børgesen, 1913:99 [as f. 'explanata'], fig. 82.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 15, 5 Apr 1976, JN-6329; sta 18, 25 Apr 1977, JN-6739.

CARIBBEAN DISTRIBUTION.—Virgin Islands (Børgesen, 1913).

### **Rhipocephalus phoenix (Ellis and Solander) Kützing**

*Rhipocephalus phoenix* (Ellis and Solander) Kützing, 1849: 506.—Taylor, 1960:174, pl. 22: figs. 2, 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, 27 Mar 1976, JN-7048; sta 4, growing among *Thalassia*, 20 Apr 1977, JN-7006; sta 9, 27 Apr 1977, JN-6411; sta 10, 29 Apr 1977, JN-6818, 25 Apr 1977, JN-6882, and 23 Apr 1977, JN-6902; sta 14, 27 Apr 1977, JN-6786.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Belize, Old Providence Island, Panama, Colombia (Taylor, 1960); Antigua (Taylor, 1969).

### \***Rhipocephalus phoenix f. brevifolius A. and E. S. Gepp**

*Rhipocephalus phoenix f. brevifolius* Gepp and Gepp, 1905:4.—Taylor, 1960:174, pl. 22: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6392, and 27 Mar 1976, JN-7049; sta 18, 25 Apr 1977, JN-6742; sta 19, 25 Apr 1977, JN-7016. South Water Cay: sta 23, 30 Apr 1979, JN-7316.

CARIBBEAN DISTRIBUTION.—Bahamas, Guadeloupe (Gepp and Gepp, 1911); Jamaica (Collins, 1909).

### \***Rhipocephalus phoenix f. longifolius A. and E. S. Gepp**

*Rhipocephalus phoenix f. longifolius* Gepp and Gepp, 1905:4.—Taylor, 1960:174, pl. 22: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 21 Apr 1977, JN-6936, and 30 Apr 1979, JN-7339; sta 4, 27 Mar 1976, JN-7050; sta 15, 5 Apr 1976, JN-6330, and 27 Apr 1977, JN-6679; sta 19, 25 Apr 1977, JN-7015.

CARIBBEAN DISTRIBUTION.—Florida (Gepp and Gepp, 1911).

### **Udotea cyathiformis Decaisne**

*Udotea cyathiformis* Decaisne, 1842:106.—Taylor, 1960:166, pl. 22: fig. 4.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 28, 29 Mar 1976, JN-6155; sta 9, 29 Apr 1977, JN-6817; sta 10, 25 Apr 1977, JN-6883.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Virgin Islands, Guadeloupe, Barbados, Panama (Taylor, 1960); Dominican Republic (Almodóvar and Bonnelly, 1977); St. Vincent (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Curaçao (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b).

### ***Udotea flabellum* (Ellis and Solander) Howe**

*Udotea flabellum* (Ellis and Solander) Howe, 1904:94.—Taylor, 1960:168, pl. 20: figs. 4, 5, pl. 25: fig. 3.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 21 Apr 1977, JN-6934; sta 10, 23 Apr 1977, JN-6919; sta 14, 5 Apr 1976, JN-6332; sta 18, 25 Apr 1977, JN-6735. Twin Cays: sta 25, 26 Apr 1977, JN-6853, JN-6854, JN-6855, and JN-6877.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Salt Key Bank, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Grenada, Belize, Panama, Colombia (Taylor, 1960); St. Kitts, Antigua, Dominica, St. Lucia, Barbados, St. Vincent (Taylor, 1969); Curaçao, Bonaire (Diaz-Piferrer, 1964a).

### **\* *Udotea cf. occidentalis* A. and E. S. Gepp**

*Udotea occidentalis* Gepp and Gepp, 1911:127–128, figs. 18, 22a-b, 63–65.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6391.

CARIBBEAN DISTRIBUTION.—Virgin Islands (Taylor, 1960).

## **Division PHAEOPHYTA**

### **Order ECTOCARPALES**

#### **Family ECTOCARPACEAE**

##### **\* *Ectocarpus elachistaeformis* Heydrich**

*Ectocarpus elachistaeformis* Heydrich, 1892:470.—Taylor, 1960: 202, pl. 29: fig. 9.—Earle, 1969:133, fig. 28.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, epiphytic on *Avrainvillea longicaulis*, 30 Mar 1976, JN-7249b.

CARIBBEAN DISTRIBUTION.—St. Thomas (Børge sen, 1914); Tobago (Taylor, 1960); Puerto Rico (Almodóvar and Blomquist, 1965); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—Representing a new record of the genus in Belize, it was found on a blade of *Avrainvillea*.

## **Order CHORDARIALES**

### **Family CHORDARIACEAE**

#### **\* *Cladosiphon occidentalis* Kylin**

FIGURE 93

*Cladosiphon occidentalis* Kylin, 1940:27.—Earle, 1969:180, figs. 72, 75, 76.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 2, epiphytic on *Thalassia*, 27 Apr 1979, JN-7648 (plurilocular sporangia). South Water Cay: sta 23, epiphytic on *Thalassia testudinum*, 30 Apr 1979, JN-7325 (plurilocular and unilocular sporangia present).

CARIBBEAN DISTRIBUTION.—Virgin Islands (Taylor, 1960); Grand Bahamas (Taylor, 1969); Panama (Earle, 1972).

REMARKS.—This is a new record of the genus in Belize.

## **Order SPHACELARIALES**

### **Family SPHACELARIACEAE**

#### **\* *Sphacelaria tribuloides* Meneghini**

*Sphacelaria tribuloides* Meneghini, 1840:2.—Taylor, 1960:211, pl. 29: fig. 6.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, epiphytic on *Turbinaria*, 30 Mar 1976, JN-7270 (fertile).

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados (Taylor,

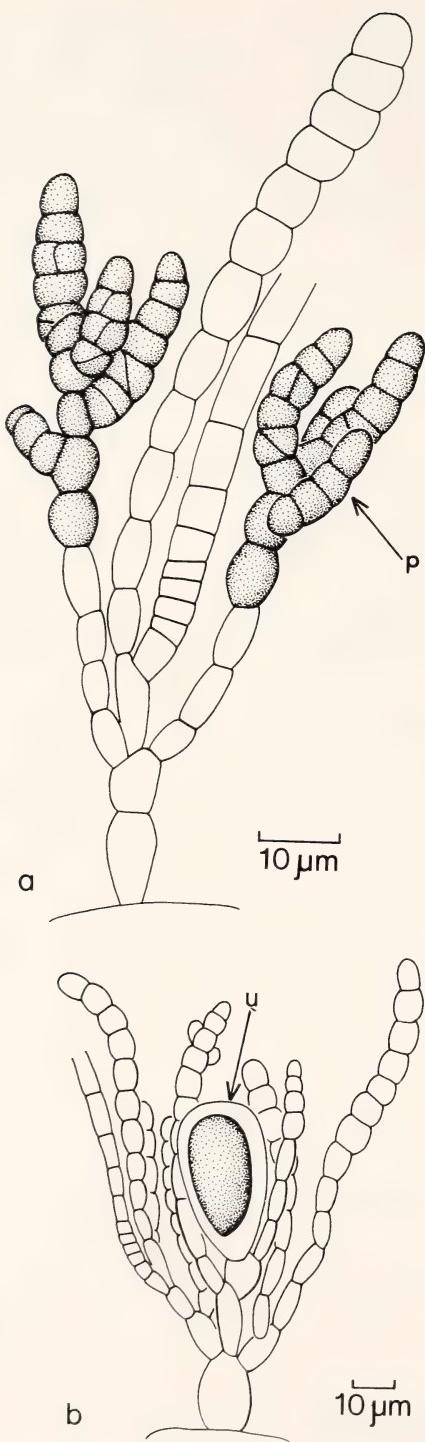


FIGURE 93.—*Cladosiphon occidentalis* (JN-7325): *a*, plurilocular sporangia (p), assimilatory filament and hairs; *b*, unilocular sporangium (u), and assimilatory filaments (plurilocular and unilocular were from same thallus).

1960); Cuba (Suarez, 1973); Antigua, Dominica (Taylor, 1969); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Trinidad (Richardson, 1975); Venezuela (Diaz-Piferrer, 1970b).

### Order DICTYOTALES

#### Family DICTYOTACEAE

##### *Dictyota bartayresii* Lamouroux

*Dictyota bartayresii* Lamouroux, 1809b:331.—Taylor, 1960: 219, pl. 30: fig. 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7011; sta 7, 23 Apr 1977, JN-6995; sta 14, 27 Apr 1977, JN-6789. South Water Cay: sta 21, 28 Apr 1977, JN-6724.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, Antigua, Guadeloupe, Dominica, Martinique, Barbados, Grenada, Panama, Colombia (Taylor, 1960); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b); Venezuela (Taylor, 1976); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Isla San Andrés (Kapraun, 1972).

##### *Dictyota cervicornis* Kützing

*Dictyota cervicornis* Kützing, 1859:11.—Taylor, 1960:222, pl. 31: fig. 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 9, 29 Apr 1977, JN-6825; sta 10, 23 Apr 1977, JN-6899, and 25 Apr 1977, JN-6970; sta 14, 27 Apr 1977, JN-6788, and 5 Apr 1976, JN-6331; sta 18, 25 Apr 1977, JN-6750. Twin Cays: sta 24, 31 Mar 1976, JN-6273; sta 25, 26 Apr 1977, JN-6870.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Barbuda, Nevis, Antigua, Guadeloupe, Martinique, Barbados, Grenadines, Belize, Panama, Colombia, Netherlands Antilles, Venezuela, Tobago (Taylor, 1960); Dominica (Taylor, 1969); Trinidad (Richardson, 1975).

### **Dictyota dichotoma (Hudson) Lamouroux**

*Dictyota dichotoma* (Hudson) Lamouroux, 1809b:331.—Taylor, 1960:218, pl. 31: fig. 5.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 15, 5 Apr 1976, JN-6339; sta 11, 25 Apr 1977, JN-6972; sta 19, 25 Apr 1977, JN-7018.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Puerto Rico, Guadeloupe, Martinique, Barbados, Grenada, Colombia, Netherlands Antilles, Venezuela (Taylor, 1960); Nevis, Antigua, St. Vincent (Taylor, 1969); Dominican Republic (Almodóvar and Bonnelly, 1977); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b); Trinidad (Richardson, 1975).

### **Dictyota divaricata Lamouroux**

*Dictyota divaricata* Lamouroux, 1809a:43.—Taylor, 1960:221, pl. 31: figs. 3, 4.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-6981; sta 10, 23 Apr 1977, JN-6918; sta 14, 27 Apr 1977, JN-6793. South Water Cay: sta 21, 28 Apr 1977, JN-6725. Twin Cays: sta 25, 26 Apr 1977, JN-6889.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Belize, Old Providence Island, Colombia, Netherlands Antilles, Trinidad (Taylor, 1960); St. Kitts, Nevis, Antigua, Dominica, St. Lucia, St. Vincent, Bequia (Taylor, 1969); Barbados (Almodóvar and Pagan, 1967); Costa Rica (Dawson, 1962b); Panama (Earle, 1972); Venezuela (Taylor, 1976); Trinidad (Richardson, 1975).

### \* **Dictyota linearis (C. Agardh) Greville**

FIGURE 94

*Dictyota linearis* (C. Agardh) Greville, 1830:xlili.—Earle, 1969:161, fig. 52.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, 31 Mar 1976, JN-6276.

**CARIBBEAN DISTRIBUTION.**—Caicos Islands, Cayman Islands, Jamaica, Hispaniola, Virgin Is-

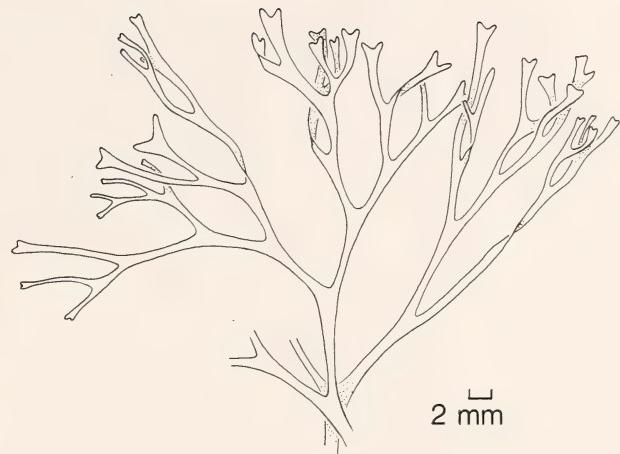


FIGURE 94.—*Dictyota linearis*, portion of the dichotomously branched frond (JN-6276), showing uneven dichotomies of the narrow frond.

lands, Guadeloupe, Netherlands Antilles (Taylor, 1960); Antigua, St. Vincent (Taylor, 1969); Venezuela (Diaz-Piferrer, 1970b).

**REMARKS.**—This taxon is distinguished primarily by its slender, dichotomous branches. Earle (1969) noted that it has forms resembling *Dictyota dichotoma*, *D. divaricata*, and *D. cervicornis* and questioned its validity as a species. Further collections in Belize are necessary before we can ascertain that it is a distinct species.

### \* **Dilophus alternans J. Agardh**

FIGURE 95

*Dilophus alternans* J. Agardh, 1882:108.—Taylor, 1960:216, pl. 30: fig. 3.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 9, 29 Apr 1977, JN-6822; sta 14, 27 Apr 1977, JN-6791.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, Barbados (Taylor, 1960); Antigua, Dominica, St. Lucia (Taylor, 1969); Curaçao (van den Hoek, 1969).

**REMARKS.**—*Dilophus* is similar in morphological appearance to *Dictyota*. The two genera are separated on anatomical differences; *Dilophus* has

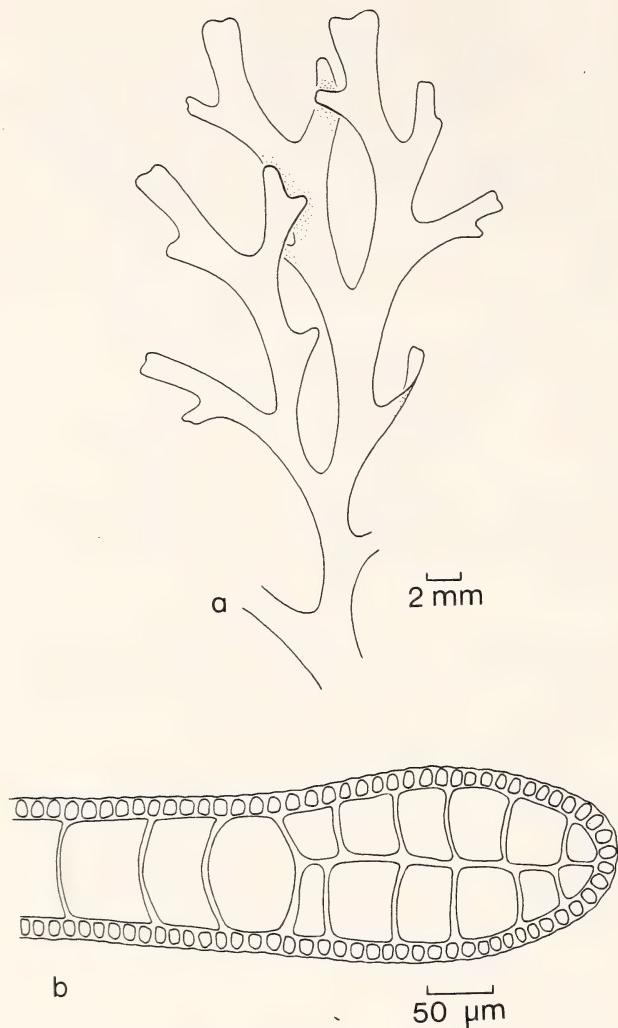


FIGURE 95.—*Diphlophus alternans* (JN-6822): *a*, portion of the thallus; *b*, transection showing a medulla more than a single cell thick along the margin, and a single layer of cortical cells.

a medulla two or more cells thick (particularly in the margins or near the base) and *Dictyota* a medulla of a single layer of cells.

#### *Dictyopteris delicatula* Lamouroux

*Dictyopteris delicatula* Lamouroux, 1809b:332.—Taylor, 1960: 227, pl. 33: fig. 3.

LOCAL DISTRIBUTION.—South Water Cay: sta 21, 28 Apr 1977, JN-6730.

CARIBBEAN DISTRIBUTION.—Mexico, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Redonda Island, Guadeloupe, Isla las Aves, Dominica, Martinique, Barbados, Grenadines, Grenada, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Trinidad, Tobago (Taylor, 1960); St. Kitts, Nevis, Antigua, St. Vincent, Bequia (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Isla San Andrés (Kapraun, 1972).

#### *Lobophora variegata* (Lamouroux) Womersley

*Lobophora variegata* (Lamouroux) Womersley, 1967:221.—Taylor, 1960:231, pl. 33: fig. 4 [as *Pocockiella variegata*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7004; sta 9, 29 Apr 1977, JN-6823, and 25 Apr 1977, JN-6974; sta 10, 23 Apr 1977, JN-6905; sta 14, 27 Apr 1977, JN-6795; sta 15, 5 Apr 1976, JN-6338, and 27 Apr 1977, JN-6696b; sta 18, 25 Apr 1977, JN-6740. Twin Cays: sta 24, 31 Mar 1976, JN-6296 and JN-6272; sta 25, 26 Apr 1977, JN-6868, and JN-6876.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, St. Eustatius, Nevis, Guadeloupe, Martinique, Barbados, Old Providence Island, Panama, Colombia (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Grand Cayman, St. Kitts, Antigua (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b); Venezuela (Taylor, 1976); Curaçao (Díaz-Piferrer, 1964b); Trinidad (Richardson, 1975).

REMARKS.—Two forms differing in thickness, color and habitat, were encountered. Dark brown, thin flattened forms, 105 to 120  $\mu\text{m}$  wide, were collected from 12 m to 14 m depths throughout the Carrie Bow Cay area (for example, JN-6974); golden brown, thicker plants with ruffled margins (120 to 180  $\mu\text{m}$  thick) were found usually in clumps in the intertidal to 1 m depths along the eastern shore of the east cay of Twin Cays (for example, JN-6876).

#### *Padina jamaicensis* (Collins) Papenfuss

*Padina jamaicensis* (Collins) Papenfuss, 1977:272.—Taylor, 1960:237, pl. 34: fig. 2 [as *P. sanctae-crucis*].

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-6982. Twin Cays: sta 24, 31 Mar 1976, JN-6269.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Anguila Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Grenada, Belize, Netherlands Antilles (Taylor, 1960); Nevis, Antigua, Dominica, Barbados, St. Vincent (Taylor, 1969); Venezuela (Diaz-Piferrer, 1970b).

### ***Padina vickersiae* Hoyt ex Howe**

*Padina vickersiae* Hoyt ex Howe, 1920b:595.—Taylor, 1960: 236, pl. 34: fig. 1.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 25, 26 Apr 1977, JN-6856.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Guadeloupe, Isla las Aves, Martinique, Barbados, Grenada, Belize, Panama, Colombia, Netherlands Antilles, Venezuela, Trinidad (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Grand Cayman, St. Kitts, Nevis, Antigua, Dominica, St. Lucia, St. Vincent (Taylor, 1969); Costa Rica (Dawson, 1962b); Isla San Andrés (Kapraun, 1972).

### ***Stylopodium zonale* (Lamouroux) Papenfuss**

*Stylopodium zonale* (Lamouroux) Papenfuss, 1940:205.—Taylor, 1960:232, pl. 28: fig. 1.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7007, and 21 Apr 1977, JN-6931; sta 2, 4 Apr 1976, JN-6303; sta 8, 29 Mar 1976, JN-6159; sta 9, 29 Apr 1977, JN-6821; sta 10, 23 Apr 1977, JN-6897; sta 11, 25 Apr 1977, JN-6880; sta 15, 5 Apr 1976, JN-6328, and 27 Apr 1977, JN-6682.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Dominica, Barbados, Panama, Colombia, Venezuela, Tobago (Taylor, 1960); Nevis, St. Vincent (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Curaçao, Bonaire (Diaz-Piferrer, 1964b).

**REMARKS.**—*Stylopodium zonale* was found growing in depths of 3 m to 28 m. Plants from greater depths (for example, JN-6328) were much thinner, about 165  $\mu\text{m}$  wide, whereas those from shallower water were thicker, to 480  $\mu\text{m}$  thick, and with more medullary cell layers (for example JN-6897).

## **Order DICTYOSIPHONALES**

### **Family PUNCTARIACEAE**

#### ***Colpomenia sinuosa* (Roth) Derbès and Solier**

*Colpomenia sinuosa* (Roth) Derbès and Solier, 1856:11.—Taylor, 1960:260, pl. 36: fig. 1.—Wynne and Norris, 1976:2, fig. 1a,b, 2a,b, 3, 11a.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, 31 Mar 1976, JN-6284.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Panama, Netherlands Antilles, Venezuela (Taylor, 1960); Dominican Republic (Almodóvar and Bonnelly, 1977); St. Kitts, Nevis, Antigua, Dominica, St. Lucia (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b); Trinidad (Richardson, 1975).

**REMARKS.**—Collected only once, this species was uncommon, at least during our spring surveys.

## **Order FUCALES**

### **Family SARGASSACEAE**

#### ***Sargassum filipendula* C. Agardh**

*Sargassum filipendula* C. Agardh, 1824:300.—Taylor, 1960: 270, pl. 37: fig. 3, pl. 40: fig. 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 21 Apr 1977, JN-6932, and 20 Apr 1977, JN-7008.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Nevis, Redonda Island, Guadeloupe, Dominica, Venezuela (Taylor,

1960); St. Kitts (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Costa Rica (Dawson, 1962b); Isla San Andrés (Kapraun, 1972); Trinidad (Richardson, 1975).

### **Sargassum fluitans Børgesen**

*Sargassum fluitans* Børgesen, 1914:66.—Taylor, 1960:281, pl. 39: fig. 2, pl. 40: fig. 7.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, drift, 31 Mar 1976, JN-6286.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Belize, Costa Rica, Panama (Taylor, 1960); Grand Cayman, St. Kitts, Nevis, Antigua, St. Lucia, Barbados (Taylor, 1969).

REMARKS.—Originally described from free-floating material (Børgesen, 1914), this species is only known in the pelagic state (Taylor, 1960; Earle, 1969).

### \* **Sargassum hystrix J. Agardh**

*Sargassum hystrix* J. Agardh, 1847:7.—Taylor, 1960:279, pl. 37: fig. 1, pl. 38: fig. 2, pl. 40: fig. 6.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 29 Mar 1976, JN-6169; sta 10, 23 Apr 1977, JN-6898; sta 14, 27 Apr 1977, JN-6790; sta 15, 5 Apr 1976, JN-6346.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Grenada, Costa Rica, Trinidad (Taylor, 1960); St. Kitts, Dominica, St. Lucia, Barbados (Taylor, 1969); Dominican Republic (Almodóvar and Bonnelly, 1977); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Venezuela (Taylor, 1976).

### \* **Sargassum hystrix var. buxifolium Chauvin**

*Sargassum hystrix* var. *buxifolium* Chauvin in J. Agardh, 1848: 322.—Taylor, 1928:128, pl. 18: fig. 1, pl. 19: fig. 9; 1960: 279, pl. 38: fig. 2, pl. 40: fig. 6.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 10, 23 Apr 1977, JN-6917; sta 11, 25 Apr 1977, JN-6971.

CARIBBEAN DISTRIBUTION.—Bahamas, Virgin Islands (Taylor, 1928); St. Lucia, Barbados (Taylor, 1969).

### **Sargassum polyceratum Montagne**

*Sargassum polyceratum* Montagne, 1837:356.—Taylor, 1960: 276, pl. 40: fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, 29 Apr 1977, JN-6378; sta 9, 29 Apr 1977, JN-6824; sta 15, 27 Apr 1977, JN-6683; sta 18, 25 Apr 1977, JN-6736.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, St. Lucia, Barbados, Old Providence Island, Panama, Colombia, Venezuela (Taylor, 1960); Antigua (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Isla San Andrés (Kapraun, 1972); Curaçao, Bonaire (Diaz-Piferrer, 1964b).

### \* **Sargassum polyceratum var. ovatum (Collins) Taylor**

*Sargassum polyceratum* var. *ovatum* (Collins) Taylor, 1928:129, pl. 18: fig. 7, 10, pl. 19: fig. 16.

LOCAL DISTRIBUTION.—South Water Cay: sta 21, 29 Apr 1977, JN-6379. Twin Cays: sta 24, 31 Mar 1976, JN-6290.

CARIBBEAN DISTRIBUTION.—Grand Cayman (Taylor, 1969); Jamaica (Collins, 1901); Hispaniola (Taylor and Arndt, 1929); Costa Rica (Dawson, 1962b); Colombia (Bula Meyer, 1977).

### **Turbinaria tricostata Barton**

*Turbinaria tricostata* Barton, 1891:218, pl. 54: fig. 3.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7005 (fertile).

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Netherlands Antilles (Taylor, 1960); Belize (Tsuda and Dawes, 1974); Isla San Andrés (Kapraun, 1972); Venezuela (Diaz-Piferrer, 1970b).

### **Turbinaria turbinata (Linnaeus) Kuntze**

*Turbinaria turbinata* (Linnaeus) Kuntze, 1898:434.—Taylor, 1960:285, pl. 39: figs. 3–5.

**LOCAL DISTRIBUTION.**—South Water Cay: sta 21, 28 Apr 1977, JN-6718 (fertile); sta 23, 30 Apr 1979, JN-7350.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Anguilla Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Antigua, Guadeloupe, Belize, Panama, Colombia, Netherlands Antilles (Taylor, 1960); Grand Cayman, St. Kitts, Nevis, Dominica (Taylor, 1969); Venezuela (Taylor, 1976).

**REMARKS.**—This species was very common in the shallow waters behind the reef crest off the north end of South Water Cay.

### **Division RHODOPHYTA**

#### **Class BANGIOPHYCEAE**

#### **Order GONIOTRICHALES**

##### **Family GONIOTRICHACEAE**

###### **\* *Goniotrichum alsidii* (Zanardini) Howe**

*Goniotrichum alsidii* (Zanardini) Howe, 1914:75.—Børgesen, 1915:4, fig. 2 [as *Goniotrichum elegans*].

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, epiphytic on *Polysiphonia*, 30 Mar 1976, JN-7265b; sta 9, epiphytic on *Sargassum*, 29 Apr 1977, JN-6838b.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Virgin Islands, Guadeloupe, Barbados, Tobago (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Curaçao (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b); Venezuela (Diaz-Piferrer, 1970b).

**REMARKS.**—This is the first report of this genus in Belize.

### **Class FLORIDEOPHYCEAE**

#### **Order NEMALIALES**

##### **Family ACROCHAETIACEAE**

###### **\* *Acrochaetium corymbiferum* (Thuret) Batters**

*Acrochaetium corymbiferum* (Thuret in Le Jolis) Batters, 1902: 59.—Taylor, 1960:312 [as *Acrochaetium bornetii*].—Dixon and Irvine, 1977:88, fig. 21 [as *Audouniella corymbifera*].

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 17, epiphytic on *Trichogloeopsis*, 25 Apr 1977, JN-7042b ( $\delta$  and monospores on same thallus).

**CARIBBEAN DISTRIBUTION.**—With this record from Belize, *Acrochaetium corymbiferum* is now added to the flora of the Caribbean Sea.

**REMARKS.**—These specimens are epiphytic on *Trichogloeopsis*, apparently a new host. Previously reported from Bermuda, North Carolina (Taylor, 1960), the Mediterranean, and England (Dixon, 1976; Dixon and Irvine, 1977), it represents a new record of the genus in Belize.

###### **\* *Acrochaetium seriatum* Børgesen**

*Acrochaetium seriatum* Børgesen, 1915:32, figs. 25–28.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 8, epiphytic on *Halimeda*, 27 Apr 1977, JN-6423b; sta 9, 29 Apr 1977, JN-6845a (monospores); sta 14, epiphytic on *Sargassum* blade, 27 Apr 1977, JN-6809a (monospores), and epiphytic on *Polysiphonia*, 5 Apr 1976, JN-6356 (monospores).

**CARIBBEAN DISTRIBUTION.**—Virgin Islands (Taylor, 1960); Costa Rica (Dawson, 1962b).

###### **\* *Acrochaetium unipes* Børgesen**

*Acrochaetium unipes* Børgesen, 1915:35, figs. 31–34.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 9, epiphytic on *Styropodium*, 23 Apr 1977, JN-6923 (monospores).

**CARIBBEAN DISTRIBUTION.**—Hispaniola, Virgin Islands (Taylor, 1960).

## Family HELMINTHOCLADIACEAE

\* *Liagora farinosa* Lamouroux

FIGURES 96a, 97

*Liagora farinosa* Lamouroux, 1816:240.—Taylor, 1960:326, pl. 43: fig. 3, pl. 45: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 29 Mar 1976, JN-6161a,b (♀), JN-6165, JN-6166, JN-6214a-e (♂), and JN-6215a-c (♂); sta 10, 25 Apr 1977, JN-6967 (♂); sta 19, 25 Apr 1977, JN-7021a,b (♀) and JN-7022 (♀).

CARIBBEAN DISTRIBUTION.—Bahamas, Turks Islands, Cuba, Cayman Islands, Jamaica, Hispan-

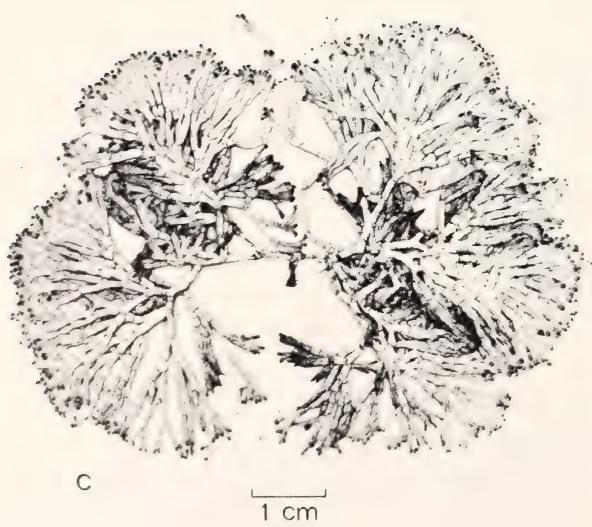
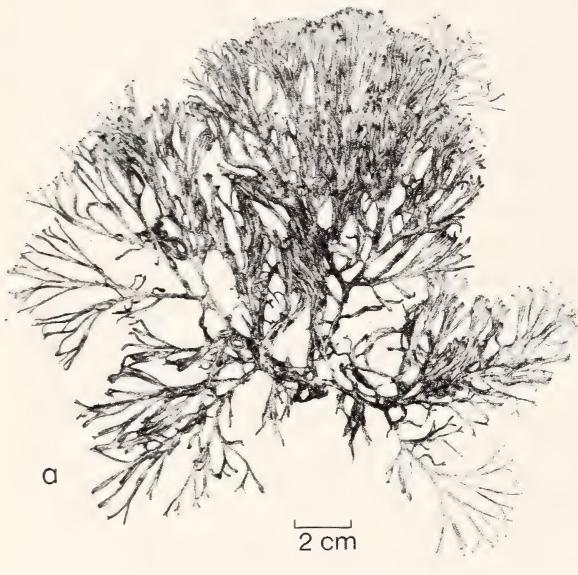


FIGURE 96.—Habits of Carrie Bow Cay species of *Liagora*: a, *L. farinosa* (JN-6161); b, *Liagora* species (JN-6216); c, *L. valida* (JN-6945); d, *L. pinnata* (JN-6163).

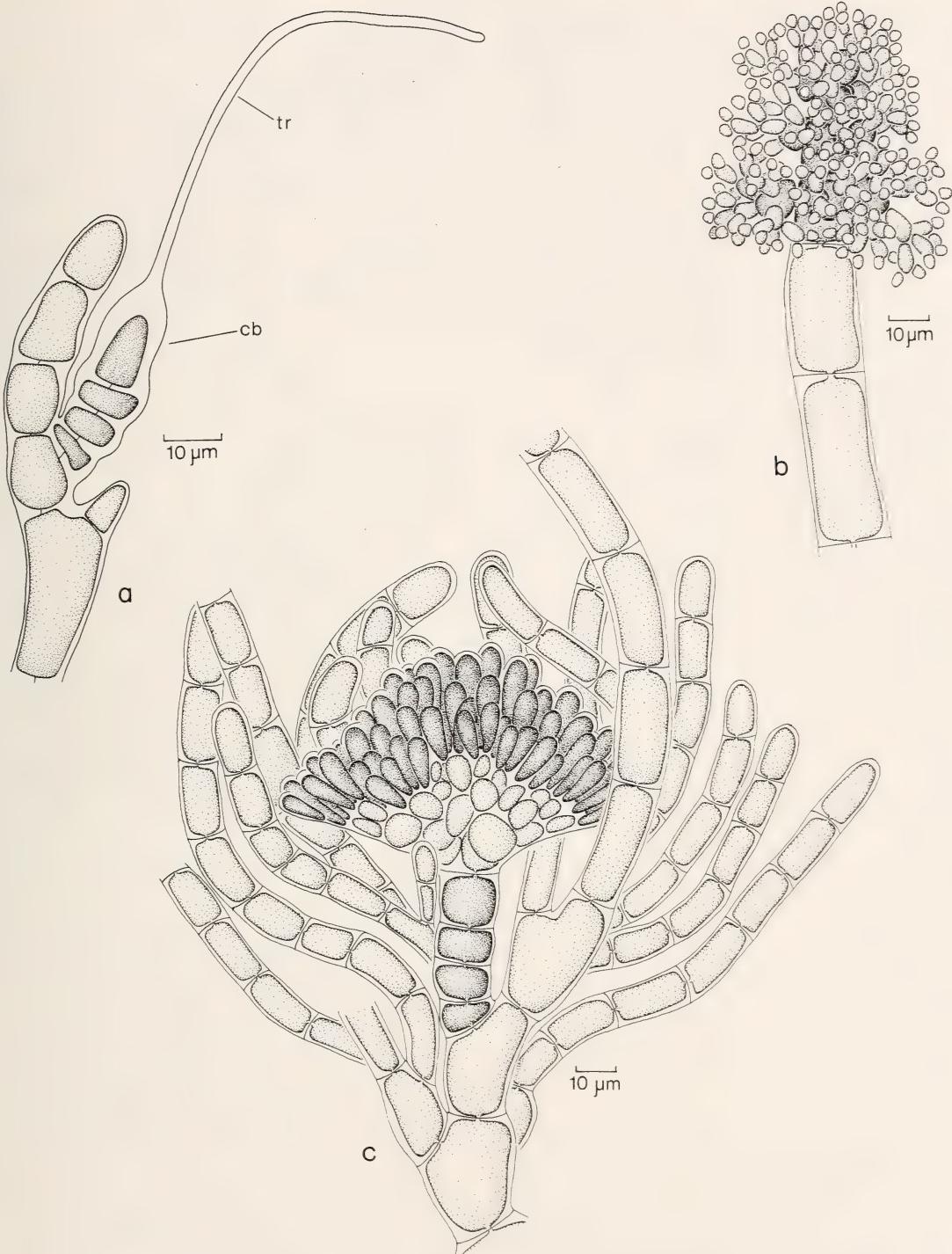


FIGURE 97.—*Liagora farinosa*, details of reproductive structures: a, carpogonial branch (cb) with trichogyne (tr) borne laterally off an assimilatory filament (JN-6161); b, an assimilatory filament with capitellate spermatangia (JN-6215b♂); c, mature cystocarp, showing portion of dense involucral filaments and large carpospores (JN-6161).

iola, Virgin Islands, Guadeloupe, Martinique, Barbados (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); St. Kitts, Nevis, St. Lucia (Taylor, 1969); Venezuela (Taylor, 1976); Curaçao (Diaz-Piferrer, 1964b; van den Hoek, 1969).

**REMARKS.**—This species is widespread throughout tropical seas (Abbott, 1945).

In describing a new genus, *Ganonema*, Fan and Wang (1974) segregated *Liagora farinosa* from other species of *Liagora* on the basis of differences in the female reproductive structure. The genus *Liagora* Lamouroux is described as having carpogonial branches borne laterally off ordinary assimilatory filaments (cf. Yamada, 1938; Abbott, 1945). *Ganonema farinosa* (Lamouroux) Fan et Wang (1974:492) bears carpogonial branches that are restricted to short filaments initiated by the basal cells of the assimilatory filaments (Fan and Wang, 1974, figs. 1–3, 6–7). This feature has previously been illustrated and noted for *L. farinosa* by Børgeesen (1927:61, figs. 33b–d) from the Canary Islands, and Yamada (1938, fig. 15) for Japanese specimens. However, none of these earlier authors gave any taxonomic or evolutionary significance to the unusual position of the carpogonial branch in *L. farinosa*. In our Belize specimens (Figure 97) we have observed carpogonial branches borne on short filaments originating off the basal cells of assimilatory filaments. Most recently Abbott (1976:130) stated, “*Liagora farinosa* has been named at least eight times (Abbott, 1945), a clear reflection of the variation shown by this species, and for lack of critical evaluation of this variation, further comparison and discussion of the generic attributes of *Ganonema* would be premature.”

#### \* *Liagora pinnata* Harvey

FIGURES 96d, 98

*Liagora pinnata* Harvey, 1853:138.—Børgeesen, 1915:74, figs. 76–81.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6941 (♀), JN-6942 (♀), and JN-6943 (♀); sta 8, 29 Mar 1976, JN-6163 (♀), JN-

6164 (♂), and JN-6213a,b (♀); sta 9, 29 Apr 1977, JN-6826 (♀).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Jamaica, Virgin Islands, Guadeloupe, Venezuela (Taylor, 1960); Cuba (Suarez, 1973); Grand Cayman (Taylor, 1969); Puerto Rico (Diaz-Piferrer, 1963), Curaçao (Diaz-Piferrer, 1964b).

**REMARKS.**—It is a widely distributed tropical species having been reported in the Pacific from China, Japan, and Hawaii (Abbott, 1945).

#### *Liagora valida* Harvey

FIGURE 96c

*Liagora valida* Harvey, 1853:138.—Taylor, 1960:327, pl. 43: fig. 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 3, 28 Apr 1977, JN-6399 (♂); sta 7, 22 Apr 1977, JN-6939 (♀), JN-6940 (♀), JN-6945 (♂); sta 9, 29 Apr 1977, JN-6828 (♀); sta 10, 23 Apr 1977, JN-6904 (♀).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Barbados, Belize, Panama (Taylor, 1960); St. Kitts, Dominica, St. Vincent (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b); Isla San Andrés (Kapraun, 1972).

**REMARKS.**—This is a wide ranging species, known from warmer waters of the Atlantic and Pacific (Abbott, 1945). Some of our Belize specimens, for instance, JN-6945 (♂), contained “monosporangial discs” among the assimilatory filaments as described by Howe (1920a) and Børgeesen (1920). These “discs,” of unknown function, would make an interesting culture investigation.

#### \* *Liagora* species

FIGURE 96b

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 8, 29 Mar 1976, JN-6176a (♀), b (♂), JN-6216 (♂), JN-6217 (♀), and 4 Apr 1976, JN-6300 (♀), JN-6301a (♀), b (♂); sta 9, 29 Apr 1977, JN-6827.

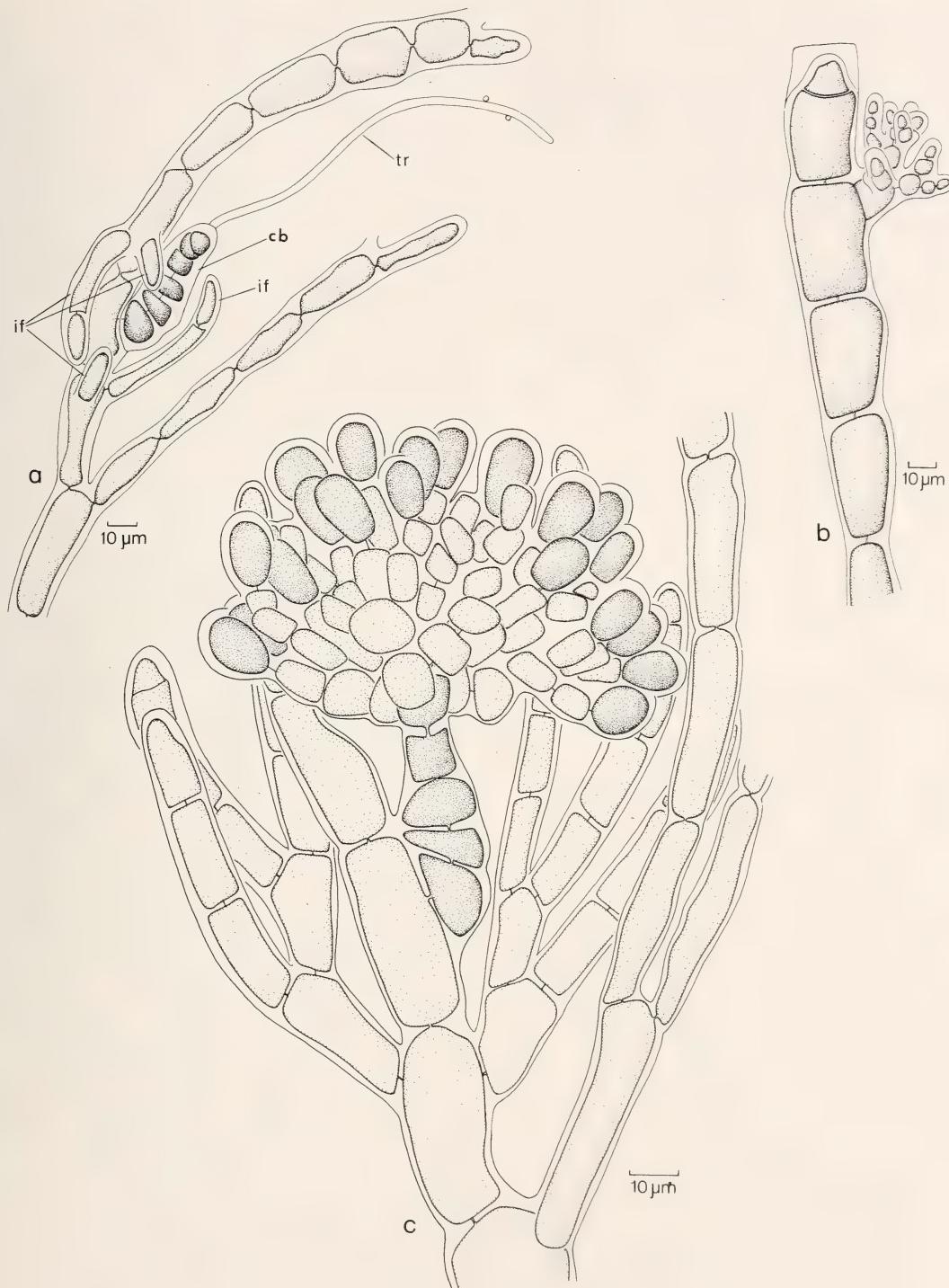


FIGURE 98.—*Liagora pinnata* (JN-6213♀), details of reproduction: *a*, carpogonial branch (cb) with trichogyne (tr; note spermatia near tip) borne laterally off an assimilatory filament, and showing developing involucral filaments (if); *b*, assimilatory filament bearing lateral spermatangia; *c*, mature cystocarp.

**REMARKS.**—The Carrie Bow Cay specimens differ in habit from other species of *Liagora* reported from the Caribbean. The carpogonial branches are formed by the modification of one of the furcations of the assimilatory filaments. They seem to represent an undescribed species; however, further material is needed to evaluate their taxonomic status.

### \**Trichogloeopsis* species

FIGURE 99

*Trichogloeopsis* cf. *pedicellata* (Howe) Abbott and Doty, 1960: 632–640, figs. 1–23.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6953 (♀), JN-6954d (♀); sta 8, 29 Mar 1976, JN-6167 (♀); sta 19, 25 Apr 1977, JN-7023 (♀), JN-7024a (♀), JN-7025 (♀), and JN-7026 (♀).

**REMARKS.**—Collections from Carrie Bow Cay represent the first record of the genus *Trichogloeopsis* in Belize. *Trichogloeopsis* Abbott and Doty (1960) is distinguished from other genera of the Helminthocladiaeae by the production of sterile rhizoids, “gonimorhizoids,” by the gonimoblast (Figure 99b). The Belizean material resembles *T. pedicellata* (Howe) Abbott and Doty (1960) in internal measurements and in being monocious.

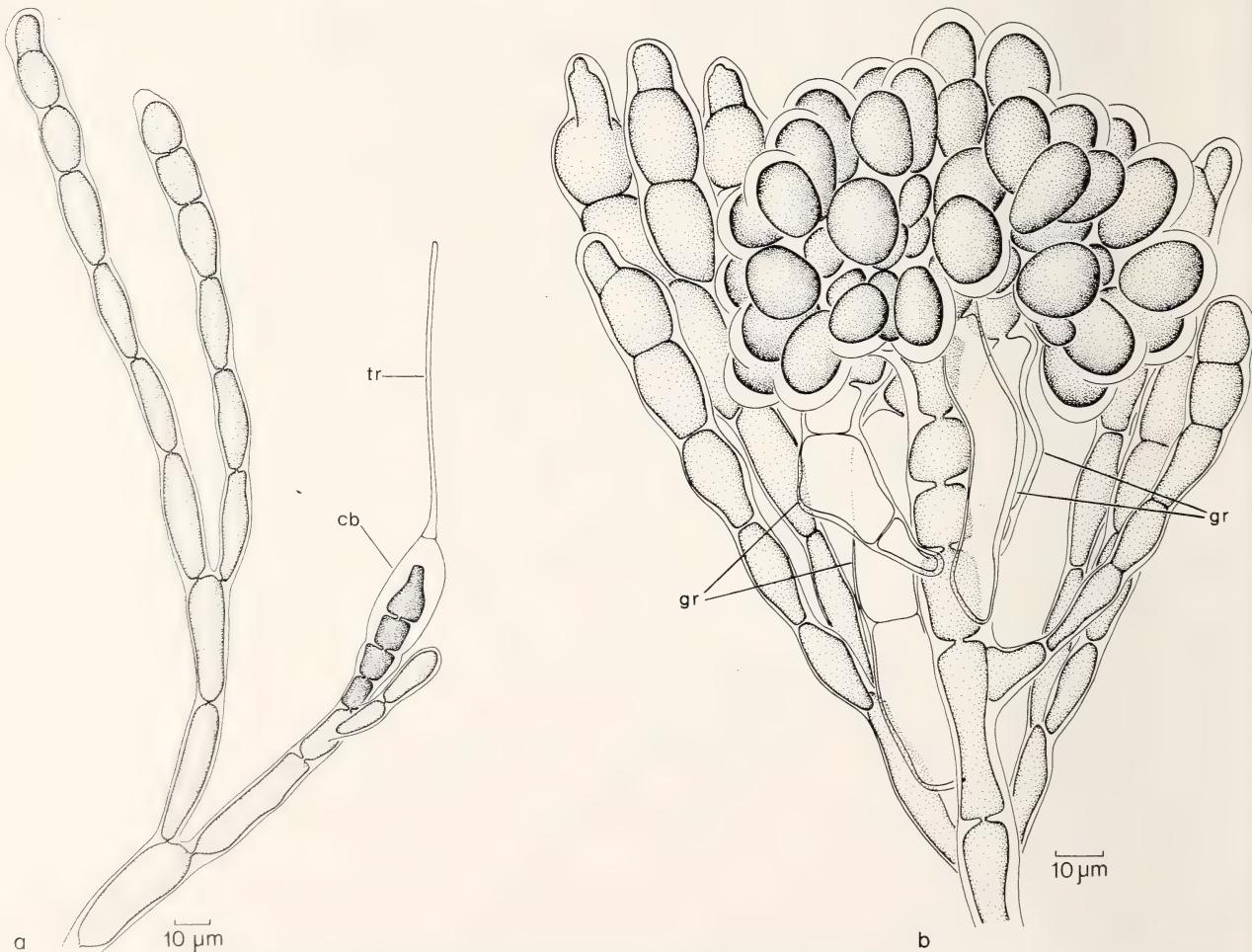


FIGURE 99.—*Trichogloeopsis* species (JN-6953), details of reproductive structures: a, carpogonial branch (cb) with trichogyne (tr) arising as a lateral (in the place of a vegetative branch) at the dichotomous branching; b, mature cystocarp with well-developed gonimoblastic rhizoids (gr).

The Belizean plants, however, differ in several respects: the assimilatory filaments are shorter in length; the cystocarps on the same thallus have both elongated (= "pedicellate" of Abbott and Doty, 1960) and non-elongated primary cells of the carpogonial branch; and the goniomoblastic rhizoids are well developed on mature cystocarps in contrast to the weakly developed ones of *T. pedicellata* (Abbott and Doty, 1960, fig. 20). A detailed study of variation in *T. pedicellata* and the Belize *Trichogloeopsis* species is needed before we can determine whether the Belize specimens are a new species or if they represent variation that could be included within *T. pedicellata*. The latter was originally described from the Bahamas as *Liagora pedicellata* Howe (1920b), and reported in Florida, Caicos Islands, Jamaica, Guadeloupe (Taylor, 1960), Barbados (Taylor, 1969), and Curaçao (van den Hoek, 1969).

### Family CHAETANGIACEAE

#### \* *Galaxaura cylindrica* (Solander) Kjellman

*Galaxaura cylindrica* (Solander) Kjellman, 1900:64.—Taylor, 1960:341, pl. 44: fig. 1.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 22 Apr 1979, JN-7404 and JN-7408.

CARIBBEAN DISTRIBUTION.—Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Barbados, Grenada, Costa Rica, Panama, Venezuela (Taylor, 1960); St. Kitts, Nevis, Dominica, St. Lucia (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b).

REMARKS.—The Carrie Bow Cay specimens are of larger diameter than is "typical" of the species, but they agree with this species in other respects. The branch diameters of *Galaxaura cylindrica* and *G. oblongata* (Ellis and Solander) Lamouroux overlap (Chou, 1947; Taylor, 1960). Chou (1947) suggested the two may prove to be one species, but Taylor (1960), while acknowledging that "branch diameters converge," stated there is little difficulty in distinguishing them. More specimens must be assembled and studied to evaluate their distinctness.

#### \* *Galaxaura lapidescens* (Ellis and Solander) Lamouroux

*Galaxaura lapidescens* (Ellis and Solander) Lamouroux, 1816: 264.—Børgeesen, 1916:95, figs. 102–104.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7013; sta 7, 22 Apr 1977, JN-6946. South Water Cay: sta 21, 28 Apr 1977, JN-6723; sta 23, 20 Apr 1979, JN-7323 and JN-7332.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Grenada, Old Providence Island, Panama, Colombia (Taylor, 1960); Dominican Republic (Almodóvar and Bonnelly, 1977); St. Lucia (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b); Venezuela (Diaz-Piferrer, 1970b).

#### \* *Galaxaura oblongata* (Ellis and Solander) Lamouroux

*Galaxaura oblongata* (Ellis and Solander) Lamouroux, 1816: 262.—Børgeesen, 1927:71, figs. 39–41.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7012, and 30 Apr 1977, JN-7342, and 30 Mar 1976, JN-7255; sta 7, 22 Apr 1977, JN-6948; sta 9, 29 Apr 1977, JN-6834; sta 10, 25 Apr 1977, JN-6973, and 23 Apr 1977, JN-6903, and 28 Apr 1979, JN-7565; sta 18, 25 Apr 1977, JN-6744; sta 19, 28 Apr 1979, JN-7620. South Water Cay: sta 21, 29 Apr 1977, JN-6382; sta 23, 30 Apr 1979, JN-7330.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Costa Rica, Panama, Trinidad (Taylor, 1960); St. Kitts, Antigua, Dominica, St. Lucia, Bequia (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964a).

REMARKS.—It is difficult to separate this species from *Galaxaura cylindrica* (see notes under that taxon), except that its branches are more than 1 mm in diameter (Taylor, 1960).

\* ***Galaxaura obtusata***  
**(Ellis and Solander) Lamouroux**

*Galaxaura obtusata* (Ellis and Solander) Lamouroux, 1816: 262.—Taylor, 1960: 342, pl. 44: figs. 4, 5, pl. 45: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 15, 27 Apr 1977, JN-6678, and 27 Apr 1979, JN-7600.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, St. Eustatius, Guadeloupe, Barbados, Tobago (Taylor, 1960); Nevis, St. Lucia (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Panama (Earle, 1972); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—At Carrie Bow Cay, it has been found only in deep-water (18–37 m) habitats.

**Family BONNEMAISONIACEAE**

\* ***Asparagopsis taxiformis* (Delile) Trevisan**

“*Falkenbergia hillebrandii*” stage of *Asparagopsis taxiformis* (Delile) Trevisan, 1845:45.—Børgesen, 1918:332, figs. 332, 333 [as *Falkenbergia hillebrandii*].—Taylor, 1960:571, pl. 72: fig. 8 [as *Falkenbergia hillebrandii*].

LOCAL DISTRIBUTION.—Twin Cays: sta 26, 29 Apr 1979, JN-7451.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Cayman Islands, Virgin Islands, Guadeloupe, Martinique, Barbados (Taylor, 1960); Cuba (Suarez, 1973); Puerto Rico (Diaz-Piferrer, 1963); Jamaica (Chapman, 1963); Antigua, Dominica (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—Only the sporophytic stage, “*Falkenbergia hillebrandii*,” was encountered at Twin Cays. This is a new Belizean record of the genus.

**Family GELIDIACEAE**

***Gelidiella acerosa* (Forsskål) Feldmann and Hamel**

*Gelidiella acerosa* (Forsskål) Feldmann and Hamel, 1934: 533.—Taylor, 1960:351, pl. 46: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6947. South Water Cay: sta 21,

entangled with *Sargassum* holdfasts, 28 Apr 1977, JN-6721, and 29 Apr 1977, JN-6380; sta 23, 30 Apr 1979, JN-7322.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Salt Key Bank, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Grenadines, Grenada, Belize, Costa Rica, Panama, Netherlands Antilles, Venezuela, Trinidad, Tobago (Taylor, 1960); Nevis, Antigua, Dominica, St. Lucia, Bequia (Taylor, 1969).

**Order CRYPTONEMIALES**

**Family DUMONTIACEAE**

\* ***Dudresnaya crassa* Howe**

*Dudresnaya crassa* Howe, 1905:572.—Taylor, 1960:364, pl. 43: fig. 6.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 29 Mar 1976, JN-6168 (♀, ♂); sta 10, 25 Apr 1977, JN-7054 (♀, ♂); sta 19, 25 Apr 1977, JN-7124.

CARIBBEAN DISTRIBUTION.—Puerto Rico (Almodóvar, 1970).

REMARKS.—Numerous specimens of this soft gelatinous species, representing a new Belizean record for the genus, were encountered subtidally at Carrie Bow Cay. *Dudresnaya crassa*, described from Bermuda by Howe (1905), has been reported to be dioecious (Taylor, 1950), but the Belizean plant is monoecious. The female and male reproductive structures and other morphological features of the Belizean specimens, however, agree with those described for *D. crassa* by Taylor (1950; 1960). One other species, *D. verticillata*, has also been reported to be both dioecious and monoecious (Taylor, 1950).

**Family RHIZOPHYLLIDACEAE**

***Ochtodes secundiramea* (Montagne) Howe**

*Ochtodes secundiramea* (Montagne) Howe 1920b:583.—Joly and Ugadim, 1966:55, pl. 1: figs. 1–8, pl. 2: figs. 1–7, pl. 3: figs. 1–4.

**LOCAL DISTRIBUTION.**—South Water Cay: sta 21, 28 Apr 1977, coll. JN, KB, W. Fenical, and O. McConnell, JN-6714, and 29 Apr 1977, JN-6895 (?).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, St. Barthélemy, Guadeloupe, Martinique, Barbados, Grenada, Belize, Costa Rica, Panama, Trinidad, Tobago (Taylor, 1960); St. Kitts, Dominica, St. Lucia, Bequia (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b).

**REMARKS.**—Many of the specimens were cystocarpic, and the cystocarps were clustered in pale wart-like nemathecia, reminiscent of parasitic algae. In fresh plants, numerous unicellular hairs issuing from the cortex of young portions were observed, as described by Joly and Ugadim (1966). Once preserved in 3% Formalin/seawater, these hairs become detached or disintegrate. The “gland cells” of fresh plants, viewed under a Wild M·5 stereo microscope, were densely interspersed throughout the cortex, and appeared iridescent blue against the red pigmented cortical cells. After methanol extraction, the “gland cells” apparently lost their contents and no longer were iridescent blue. McConnell and Fenical (1978) discovered halogenated compounds in this plant, one of which, ochotodene, was up to 50% of the crude organic extract. These “gland cells” are the probable site of halogenation storage as they have been discovered to be in another red alga, *Laurencia snyderae* (Young et al., 1980).

### Family KALLYMENIACEAE

#### \* *Kallymenia limminghii* Montagne

*Kallymenia limminghii* Montagne, 1860:173.—Taylor, 1960: 432, pl. 80: fig. 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 12, 29 Apr 1977, coll. M. Danty, JN-7105; sta 13, 23 Apr 1979, JN-7701, JN-7702, JN-7703; sta 15, 27 Apr 1979, JN-7596; sta 18, 28 Apr 1979, JN-7622.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Guadeloupe (Taylor, 1969); Puerto Rico (Almodóvar, 1970).

**REMARKS.**—Our material was found only epizoic on dead gorgonians, and is the first record of the genus in Belize.

### Family CORALLINACEAE

#### Articulate Corallinaceae

##### \* *Amphiroa fragilissima* (Linnaeus) Lamouroux

*Amphiroa fragilissima* (Linnaeus) Lamouroux, 1816:298.—Taylor, 1960: 403, pl. 47: figs. 1, 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 6, 23 Apr 1979, JN-7671a; sta 19, 25 Apr 1977, JN-7019; sta 20, 22 Apr 1979, JN-7745. Twin Cays: sta 25, epiphytic on *Halimeda*, 26 Apr 1977, JN-6873; sta 26, 29 Apr 1979, JN-7311, JN-7534.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Dominica, Martinique, Barbados, Grenadines, Grenada, Belize, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Tobago (Taylor, 1960); Grand Cayman, Nevis, Antigua, St. Lucia, Bequia (Taylor, 1969); Trinidad (Richardson, 1975).

##### \* *Amphiroa rigida* var. *antillana* Børgesen

*Amphiroa rigida* var. *antillana* Børgesen, 1917:182.—Taylor, 1960:404, pl. 47: fig. 3, pl. 48: fig. 1.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 21 Apr 1979, JN-7752; sta 10, mixed with *A. tribulus*, 28 Apr 1979, JN-7567.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Barbados, Belize, Panama (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Puerto Rico (Almodóvar, 1964); Antigua, Dominica (Taylor, 1969); Costa Rica (Dawson, 1962b); Curaçao (van den Hoek, 1969); Venezuela (Taylor, 1976).

##### \* *Amphiroa tribulus* (Ellis and Solander) Lamouroux

*Amphiroa tribulus* (Ellis and Solander) Lamouroux, 1816: 302.—Taylor, 1960:406, pl. 47: figs. 4, 5.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 21 Apr 1979, JN-7754; sta 6, 23 Apr 1979, JN-7682; sta 9, 29 Apr 1977, JN-6835; sta 14, 5 Apr 1976, coll. JN and W. Fenical, s.n.; sta 19, 28 Apr 1979, JN-7625.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Martinique, Belize, Panama (Taylor, 1960); Nevis (Taylor, 1969); Costa Rica (Dawson, 1962b); Trinidad (Richardson, 1975).

#### \* *Jania capillacea* Harvey

*Jania capillacea* Harvey, 1853:84.—Taylor, 1960:412, pl. 49: fig. 4.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, epiphytic on *Turbinaria*, 30 Mar 1976, JN-7268; sta 6, 23 Apr 1979, JN-7655b, JN-7672a; sta 7, 21 Apr 1977, JN-7129a, and 23 Apr 1977, JN-6993; sta 9, 23 Apr 1977, JN-6929; sta 10, 25 Apr 1977, JN-7218b.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, Barbados, Belize, Costa Rica, Panama, Colombia (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Grand Cayman, St. Kitts, Antigua, Dominica, St. Lucia, Grenada (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b).

#### Non-articulate Corallinaceae†

##### \* *Fosliella farinosa* (Lamouroux) Howe

*Fosliella farinosa* (Lamouroux) Howe, 1920b:587.—Masaki and Tokida, 1960:39, pl. 1: figs. 4–5, pl. 2: figs. 8–12, pls. 6–7.—Ugadim, 175:119, pl. 3: figs. 1–2

**LOCAL DISTRIBUTION.**—South Water Cay: sta 21, epiphytic on *Laurencia*, 29 Apr 1977, JN-6381b.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba,

Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Barbados, Belize, Old Providence Island, Costa Rica, Panama, Colombia, Venezuela, Netherlands Antilles, Tobago (Taylor, 1960); St. Kitts, Antigua, St. Lucia, Dominica, Bequia (Taylor, 1969).

#### \* *Fosliella* species 1

**LOCAL DISTRIBUTION.**—South Water Cay: sta 21, epiphytic on *Laurencia*, 29 Apr 1977, JN-6381c.

**REMARKS.**—This epiphyte has cells (7–15 µm long) and tetrasporangia (30–42 µm long) that are much smaller than those of *Fosliella farinosa*, which has larger cells (12–30 µm long) and tetrasporangia (40–90 µm long). Therefore it represents a different species. See generic comments below.

#### \* *Fosliella* species 2

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 6, epilithic on coral rubble, 23 Apr 1979, JN-7668 (Z).

**REMARKS.**—Before species names can be confidently placed on uniporate, thin crusted non-articulate corallines, the problems with the circumscription of the genera *Fosliella* and *Heteroderma* must be resolved. At this time, it seems best to refer to the two unknown Belizean species of *Fosliella* as *F. species 1* and *F. species 2*.

#### \* *Lithoporella atlantica* (Foslie) Foslie

*Lithoporella atlantica* (Foslie) Foslie, 1909:59; 1929, pl. 73: fig. 9.—Taylor, 1960: 387 [as *Fosliella atlantica*].

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, epilithic on coral rubble, 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7512 (Z).

**CARIBBEAN DISTRIBUTION.**—Virgin Islands, Hispaniola (Taylor, 1960).

**REMARKS.**—From the Caribbean collections of W. H. Adey (Coralline Herbarium, US), this species appears in few localities and where found, is apparently not abundant. It is a new Belizean record for the genus.

† Contributed by Roberta A. Townsend, School of Biological Sciences, University of Sydney, Sydney 2006, New South Wales, Australia (work completed while author was on a Smithsonian Institution Predoctoral Fellowship, National Museum of Natural History, Washington, D.C. 20560).

\* ***Hydrolithon boergesenii* (Foslie) Foslie**

*Hydrolithon boergesenii* (Foslie) Foslie, 1909:56.—Taylor, 1960: 397, pl. 76: fig. 2 [as *Goniolithon boergesenii*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, epilithic on coral rubble, 23 Apr 1979, JN-7669 and JN-7670a, and 10 May 1978, coll. K. Rützler, s.n.

CARIBBEAN DISTRIBUTION.—Dominican Republic, Virgin Islands, Barbados, Costa Rica (Taylor, 1969); Nicaragua (Dawson, 1962b).

REMARKS.—In the Caribbean, this species is common throughout the intertidal zone and may be found to a depth of 67 m. This is the first report of the genus in Belize.

\* ***Mesophyllum* species 1**

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 14, on coral rubble, 27 Apr 1979, JN-7589.

REMARKS.—Unfortunately this specimen is not reproductive; however, it has a leafy habit, thick coaxial hypothallium, "large-celled" meristem (cf. Adey and Macintyre, 1973), and rounded epithallial cells. It also lacks heterocysts; therefore I place it into the genus *Mesophyllum*. A new record of the genus in Belize, this specimen represents a new species that is under study by W. H. Adey (pers. comm.).

\* ***Neogoniolithon strictum* (Foslie) Setchell and Mason**

*Neogoniolithon strictum* (Foslie) Setchell and Mason, 1943:92.—Taylor, 1960:399, pl. 48: fig. 4, pl. 77: figs. 1-2 [as *Goniolithon strictum*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7501, and 23 Jun 1977, coll. K. Rützler, CBC-77.6.23.

CARIBBEAN DISTRIBUTION.—Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands (Taylor, 1960); Curaçao (van den Hoek, 1969).

REMARKS.—This material has the sloughing epithallium characteristic of *Neogoniolithon strictum*. A rather common species at Carrie Bow Cay, it is free living among *Thalassia* on the reef flat

seaward of the IMSWE laboratory. A new generic record for Belize, this is apparently the first record of this taxon from the Central America coast of the Caribbean.

\* ***Neogoniolithon* species 1**

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, 23 Apr 1979, JN-7670b (Z).

REMARKS.—This specimen is regularly branched, and grows sympatrically with *Hydrolithon boergesenii* on the same coral rubble. It possesses a coaxial hypothallium, single heterocysts, and conceptacles of 750 µm outside diameter.

*Neogoniolithon* species 1 and 2 are under study by W. H. Adey and represent undescribed species (pers. comm.)

\* ***Neogoniolithon* species 2**

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, on coral surface, 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7499.

REMARKS.—A non-branched *Neogoniolithon*, with a parallel hypothallium that is coaxial in places. The conceptacles range from 250 to 500 µm outside diameter. See also comments on *N. species 1* above.

\* ***Porolithon pachydermum*  
(Weber-van Bosse and Foslie) Foslie**

*Porolithon pachydermum* (Weber-van Bosse and Foslie in Foslie, 1909:57; 1929, pl. 67: figs. 9-10.—Taylor, 1960: 401.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, on coral face, 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7498 (Z).

CARIBBEAN DISTRIBUTION.—Jamaica, Puerto Rico, Virgin Islands, Barbados (Taylor, 1960); Curaçao (van den Hoek, 1969).

REMARKS.—This crust has the definite heterocyst fields found in the type of *Porolithon pachydermum* (isotype number FT-121, Coralline Herbarium, US). This species is common in shallow waters to depths of 20 m on Caribbean outer reefs

(W. H. Adey, pers. comm.), and represents a genus new to Belize.

### Order GIGARTINALES

#### Family GRACILARIACEAE

##### \* *Gracilaria crassissima* P. and H. Crouan

FIGURE 100

*Gracilaria crassissima* P. and H. Crouan in Mazé and Schramm, 1878:218.—Taylor, 1960: 443, pl. 55: fig. 4, pl. 57: fig. 4.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6996.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica, Hispaniola, Puerto Rico, Guadeloupe (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); St. Lucia, Grenada (Taylor, 1969); Barbados (Almodóvar and Pagan, 1967); Curaçao (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b); Panama (Earle, 1972).

REMARKS.—The fresh specimen measured 14 cm in diameter, approximately 8 cm in height, and up to 5 cm in width, individual fronds were

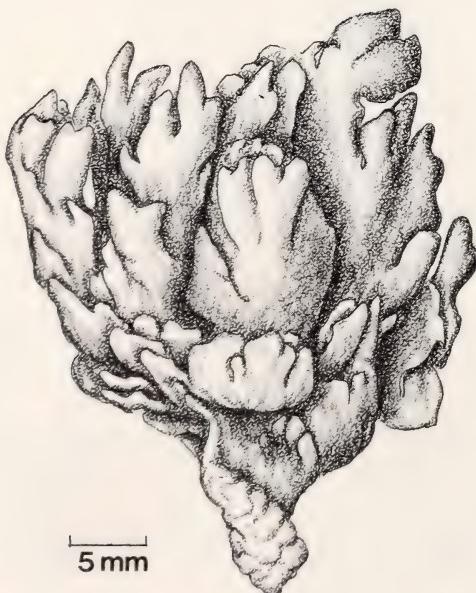


FIGURE 100.—*Gracilaria crassissima*, habit of a portion of a robust specimen (JN-6996).

up to 1.3 cm in thickness. It was growing on the reef crest in shallow water, attached to the underside of a large piece of dead *Acropora palmata* coral in an area of strong swells and surge.

#### Family SOLIERIACEAE

##### \* *Eucheuma? echinocarpum* Areschoug

*Eucheuma echinocarpum* Areschoug, 1854:349 [= reprint p. 23].—Taylor, 1960:458.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6960 (Z).

CARIBBEAN DISTRIBUTION.—Cuba (Diaz-Piferrer, 1964a; Suarez, 1973); Jamaica (Collins, 1901; Chapman, 1963); Dominican Republic (Almodóvar and Bonnelly, 1977); Puerto Rico (Almodóvar, 1964); Guadeloupe (Taylor, 1960); Nevis, Dominica (Taylor, 1969); Barbados (Almodóvar and Pagan, 1967); Curaçao (van den Hoek, 1969); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—The correct generic placement of this taxon is currently under study by D. Cheney (pers. comm.).

##### \* *Eucheuma? cf. schrammii* (P. and H. Crouan J. Agardh)

FIGURE 101

*Eucheuma schrammii* (P. and H. Crouan in Schramm and Mazé) J. Agardh, 1892:124.—Taylor, 1960:458.—Diaz-Piferrer, 1970a:12, fig. 6.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-7106 (♀).

CARIBBEAN DISTRIBUTION.—Virgin Islands, Guadeloupe (Taylor, 1960); Puerto Rico (Almodóvar, 1970); Dominica (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b); Venezuela (Diaz-Piferrer, 1970b).

REMARKS.—In habit, the Carrie Bow Cay plant resembles both *Eucheuma schrammii* and *Meristotheca tobagensis* Taylor (1962b:55). Examination of mature cystocarps from the type of *M. tobagensis* (Taylor, 1962b, pl. 4: fig. 1; holotype number US-33935) revealed a structure like that described and illustrated for the type of the genus, *M.*

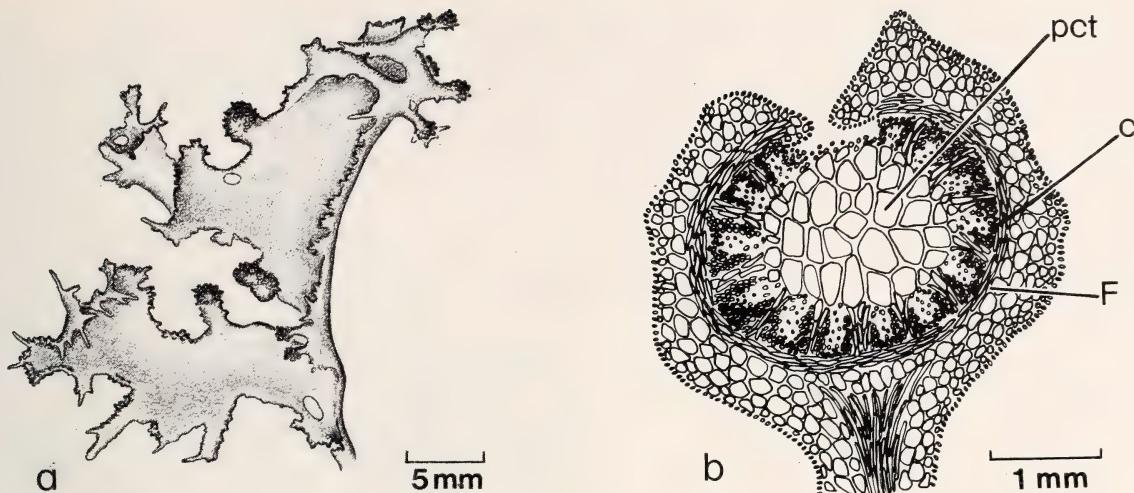


FIGURE 101.—*Eucheuma?* cf. *schrammii* (JN-7106): *a*, habit of a portion of the thallus showing spiny nature of mature cystocarps; *b*, cross section through a mature cystocarp showing parenchymatous central tissue (pct), and the gonimoblast and carposporangia (c) developing outward towards the “Faserhülle” (F).

*papulosa* (Montagne) J. Agardh, by Børgesen (1934b:13–16, fig. 11). Mature cystocarps of both *M. papulosa* and *M. tobagensis* have gonimoblast tissue and carposporangia developing outward from the parenchymatous central tissue. Similarly, in cystocarps of the Carrie Bow Cay specimen, the gonimoblast and carposporangia appear to develop outwards towards the “Faserhülle” from the parenchymatous central tissue (Figure 101*b*). Therefore, we suggest that the taxon *E. schrammii* is probably a *Meristotheca*. However, until the type of *Mychodea schrammii* is re-examined to determine if its cystocarpic construction and carposporangial development is the same as our Belizean plant, we tentatively identify the latter as *E.?* cf. *schrammii*.

Recently, Cheney and Dawes (in press) examined the “Originalexemplar” of *Eucheuma schrammii* selected by Kylin (1932, pl. 10: fig. 23) (*Mychodea schrammii* P. and H. Crouan in Schramm and Mazé 1865:10; Herbarium Agardh number 34680, LD) and concluded that this taxon is not a *Eucheuma* (a genus in which the mature cystocarps possess a single fusion cell). The generic placement of *M. schrammii* is under study by D. Cheney (pers. comm.).

Taylor (1960:458) has described the cystocarps of *Eucheuma schrammii* as “hardly projecting from the surface, but the overlaying tissue often apiculate.” Cystocarps of the Belizean plant differ in being confined to marginal portions of the blade; they also are very spiny (Figure 101*a*). More Caribbean material must be studied, particularly from the type locality in Guadeloupe, to assess the importance of these features for taxonomic purposes.

#### Family CAULACANTHACEAE

Guiry (1978:193) has recently pointed out that the family name Caulacanthaceae Kützing (1843) has nomenclatural priority over Rhabdoniaceae Kylin (1925).

#### *Catenella repens* (Lightfoot) Batters

*Catenella repens* (Lightfoot) Batters, 1902:69.—Taylor, 1960: 462, pl. 66: fig. 13.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, 31 Mar 1976, JN-6293c and JN-6295, and 26 Apr 1977, JN-6872.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba,

Jamaica, Virgin Islands, Tortola Island, Guadeloupe, Martinique, Belize, Panama (Taylor, 1960); Puerto Rico (Almodóvar, 1965); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b); Trinidad (Richardson, 1975).

**REMARKS.**—This species, a new Belizean record for the genus, was found in association with *Bos-trychia*, growing on mangrove roots; its common habitat in the Caribbean.

#### Family HYPNEACEAE

##### *Hypnea cervicornis* J. Agardh

*Hypnea cervicornis* J. Agardh, 1852:451.—Taylor, 1960:466, pl. 73: fig. 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 3, entangled with *Laurencia*, 28 Apr 1977, JN-6395 (♀); sta 7, 21 Apr 1977, JN-6983. Twin Cays: sta 24, 31 Mar 1976, JN-6299 (θ); sta 25, 26 Apr 1977, JN-6893.

**CARIBBEAN DISTRIBUTION.**—Mexico, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Belize, Panama, Colombia, Netherlands Antilles, Venezuela (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Antigua, Barbados, Grenada (Taylor, 1969); Costa Rica (Dawson, 1962b); Trinidad (Richardson, 1975).

**REMARKS.**—Bisporangia, 15–23  $\mu\text{m} \times$  45–52  $\mu\text{m}$ , borne in specialized branches were found on JN-6299; the usual mode of sporophyte reproduction is by zonate tetraspores.

##### *Hypnea musciformis* (Wulfen) Lamouroux

*Hypnea musciformis* (Wulfen) Lamouroux, 1813:131.—Taylor, 1960:467, pl. 73: fig. 1.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, 31 Mar 1976, JN-6271.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Barbados, Grenada, Belize, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Trinidad, To-

bago (Taylor, 1960); St. Kitts, Nevis, Antigua, Dominica, St. Lucia, St. Vincent, Bequia (Taylor, 1969); Isla San Andrés (Kapraun, 1972).

#### Order RHODYMENIALES

##### Family RHODYMENIACEAE

###### \* *Botryocladia shanksii* Dawson

*Botryocladia shanksii* Dawson, 1962b:385, pl. 2: figs. A, B, pl. 5: fig. B.—Schnetter, 1977:79, figs. 8–11.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 20 Apr 1977, JN-7107.

**CARIBBEAN DISTRIBUTION.**—Barbados, Costa Rica (Dawson, 1962b); Colombia (Schnetter, 1977).

##### Family CHAMPIACEAE

###### *Champia parvula* (C. Agardh) Harvey

*Champia parvula* (C. Agardh) Harvey, 1853:76.—Taylor, 1960:490, pl. 61: fig. 4.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 3, epiphytic on *Udotea*, 28 Apr 1977, JN-6400; sta 6, epiphytic on *Thalassia*, 23 Apr 1979, JN-7651; sta 8, epiphytic on *Halimeda*, 27 Apr 1977, JN-6420 (⊕), JN-6435 (♀); sta 9, 29 Apr 1977, JN-6846a; sta 10, 23 Apr 1977, JN-6922; sta 11, epiphytic on *Sargassum*, 29 Mar 1976, JN-6175; sta 14, epiphytic on *Sargassum hystrix*, 5 Apr 1976, JN-6350 (⊕) and epiphytic on *Dictyota dichotoma*, JN-6340 (⊕), and 27 Apr 1977, JN-6804; sta 15, epiphytic on *Sargassum* blade, 27 Apr 1977, JN-6689 (♀); sta 18, 25 Apr 1977, JN-6752 (♀⊕).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Dominica, Barbados, Venezuela (Taylor, 1960); Cuba (Suarez, 1973); Nevis, Antigua (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Costa Rica (Wellington, 1973).

**REMARKS.**—In 1976 and 1977 *Champia parvula* was found at several stations in the vicinity of Carrie Bow Cay, but it was always sparse in distribution and coverage. In the spring of 1979,

however, this species appeared in great abundance as an epiphyte on *Thalassia* at station 6, a dominant yellow coverage seen over the entire reef flat (compare Rützler and Macintyre, herein: 15, Figures 6b, 7b).

### ***Coelothrix irregularis* (Harvey) Børgesen**

*Coelothrix irregularis* (Harvey) Børgesen, 1920:389.—Taylor, 1960:488, pl. 45: fig. 3, pl. 46: fig. 4.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 6, 23 Apr 1979, JN-7658 and JN-7666.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Belize (Taylor, 1960); Grand Cayman, Antigua, Dominica, St. Lucia, Barbados (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Trinidad (Richardson, 1975).

### \* ***Chrysymenia* cf. *okamurai* Yamada and Segawa**

*Chrysymenia okamurai* Yamada and Segawa, 1953:110, fig. 3.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, 27 Apr 1977, JN-6428.

REMARKS.—This species represents a genus not previously recorded in Belize, and is apparently not known elsewhere in the Caribbean. The plant resembles *Chrysymenia okamurai* Yamada and Segawa (1953:110, fig. 3; see also Abbott and Littler, 1969) from Japan and Hawaii in general morphology. More specimens, however, particularly cystocarpic ones, are needed before the identity of the Belize alga can be established.

### Order CERAMIALES

#### Family CERAMIACEAE

##### ***Antithamnion ogdeniae* Abbott**

*Antithamnion ogdeniae* Abbott, 1979:218, figs. 11–14.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, epiphytic on *Halimeda*, 27 Apr 1977, JN-6429 and

JN-6430; sta 14, epiphytic on *Sargassum*, 5 Apr 1976, JN-6347.

CARIBBEAN DISTRIBUTION.—This species was recently described from St. Croix, U.S. Virgin Islands, and Belize, with specimens (paratypes) from Carrie Bow Cay (Abbott, 1979).

### \* ***Antithamnionella flagellata* (Børgesen) Abbott**

*Antithamnionella flagellata* (Børgesen) Abbott, 1979:222, figs. 18–20 [as '*flagellatum*'].—Børgesen, 1945:5, figs. 1, 2 [as *Antithamnion flagellatum*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, epiphytic, 27 Apr 1977, JN-6427 (⊕); sta 9, epiphytic, 29 Apr 1977, JN-6841d.

CARIBBEAN DISTRIBUTION.—Virgin Islands (Abbott, 1979).

REMARKS.—This species was originally described from Mauritius (Børgesen, 1945) and only recently found near St. Croix, U.S. Virgin Islands (Abbott, 1979). Belizean specimens (the first record of the genus in Belize), while in general agreement with *Antithamnionella flagellata*, have branchlets reaching only 300 µm in length, shorter than the 300–600 µm length previously described.

### ***Centroceras clavulatum* (C. Agardh) Montagne**

FIGURE 102

*Centroceras clavulatum* (C. Agardh) Montagne, 1846:140.—Abbott and Hollenberg, 1976:604, fig. 547.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, epiphytic on *Laurencia*, 28 Apr 1977, JN-6394; sta 7, entangled with turf, 23 Jun 1977, coll. K. Rützler, CBC-77.6.23, and in algal turf, intermixed with *Anotrichium tenuie*, *Jania* and *Ceramium*, 22 Apr 1977, JN-6958b, and in algal turf, entangled with *Taenioma*, *Herposiphonia*, and *Jania*, JN-6989a (♂); sta 15, 27 Apr 1977, JN-6688a. South Water Cay: sta 21, on concrete block, 29 Apr 1977, JN-6384. Twin Cays: sta 26, 22 Apr 1979, JN-7435.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica,

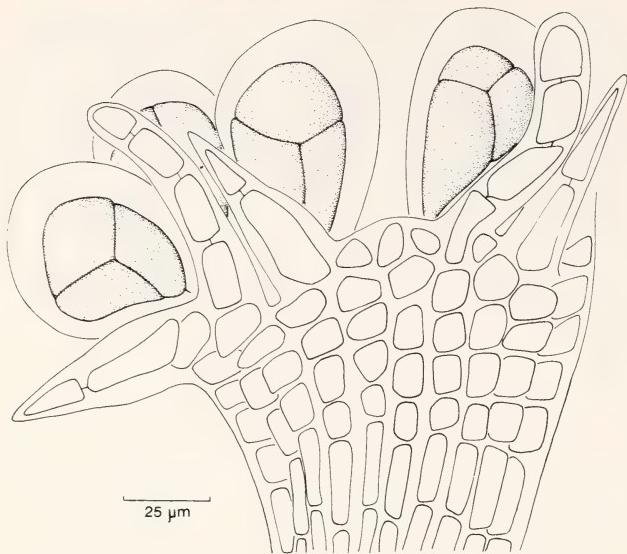


FIGURE 102.—*Centroceras clavulatum*, upper portion of thallus, showing node with emergent tetrasporangia subtended by spines and involucres (JN-6384).

Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Dominica, Martinique, Barbados, Grenada, Belize, Old Providence Island, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Tobago (Taylor, 1960); St. Kitts, Antigua, St. Lucia, St. Vincent, Bequia (Taylor, 1969); Isla San Andrés (Kapraun, 1972); Trinidad (Richardson, 1975).

**REMARKS.**—*Centroceras clavulatum* apparently has variable tetrasporangia as well as vegetative morphology. Tetrasporangia of the Belize specimens are emergent, subtended by 2-3 celled spines and occasionally by 4- to 5-celled involucres (Figure 102). Taylor (1960:537) describes the tetrasporangia as mostly exposed, generally formed in the whorl of spines, but does not mention involucres, while Joly (1965, pl. 39: fig. 502) illustrates the tetrasporangia of material from Brasil with involucres but without spines.

#### \* *Ceramium brevizonatum* var. *caraibicum* H. Petersen and Børgesen

*Ceramium brevizonatum* var. *caraibicum* H. Petersen and Børgesen in Børgesen, 1924:29 [as 'caraibica'].—Taylor, 1960: 527, pl. 67: figs. 7-9.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6988 (♂), and epiphytic on *Liagora*, JN-6955c (⊕,♀). South Water Cay: sta 21, 28 Apr 1977, JN-6732 (⊕).

**CARIBBEAN DISTRIBUTION.**—Hispaniola (Taylor, 1960); Antigua, Barbados (Taylor, 1969).

#### \* *Ceramium fastigiatum* f. *flaccidum* H. Petersen

*Ceramium fastigiatum* f. *flaccidum* H. Petersen in Børgesen, 1918:242 [as f. 'flaccida'].—Taylor, 1960:527, pl. 67: figs. 4-6.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 15, 5 Apr 1976, epiphytic on *Dictyota dichotoma*, JN-6343 (♀), and epiphytic on *Dictyota cervicornis*, JN-6336, and 27 Apr 1977, JN-6688b (♂) and JN-6690 (⊕,♂).

**CARIBBEAN DISTRIBUTION.**—Jamaica (Chapman, 1963); Hispaniola (Taylor and Arndt, 1929); Virgin Islands (Børgesen, 1918); Guadeloupe (Feldman and Lami, 1935).

#### \* *Ceramium flaccidum* (Kützing) Ardisson

*Ceramium flaccidum* (Kützing) Ardisson, 1871:40.—Dawson, 1962a:57, pl. 20: figs. 2-3, pl. 21: figs. 2-3 [as *C. gracillimum* var. *byssoides*].—Womersley, 1978:234, figs. 4a-d.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 3, epiphytic on *Udotea*, 28 Apr 1977, JN-6402 (⊕); sta 7, 22 Apr 1977, epiphytic on *Liagora*, JN-6957 (♀); sta 8, epiphytic on *Sargassum*, 29 Mar 1976, JN-6173 (♀), and epiphytic on *Caulerpa*, 27 Apr 1977, JN-6415a (⊕) and JN-6431 (⊕); sta 9, epiphytic on *Sargassum*, 29 Apr 1977, JN-6843 (⊕); sta 10, epiphytic on *Dictyota*, 23 Apr 1977, JN-6910 (⊕), JN-6912 (⊕), JN-7212 (⊕); sta 17, 25 Apr 1977, JN-6754b (♀), JN-6759a (⊕) and epiphytic on *Dictyota*, JN-6747 (⊕,♂). Twin Cays: sta 24, epiphytic on *Stylopodium*, 26 Apr 1977, JN-6884 (⊕,♀).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, Saba Bank, Old Providence Island, Colombia, Venezuela (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Barbados (Taylor, 1969); Curaçao (Díaz-Piferrer,

1964b); Costa Rica (Dawson, 1962b).

**REMARKS.**—This minute species is commonly found on a variety of coarser algae. It is a wide-ranging species, found in the Pacific (Taylor, 1945, as *Ceramium byssoides*; Dawson, 1961, as *C. gracillimum* var. *byssoides*), Gulf of California (Dawson, 1962a, as *C. gracillimum* var. *byssoides*), Caribbean (Taylor, 1960, 1969, as *C. byssoides*), Australia (Womersley, 1978), North Africa (Mazoyer, 1938, as *C. gracillimum* var. *byssoides*), and Europe (Feldmann-Mazoyer, 1941, as *C. gracillimum* var. *byssoides*). Womersley (1978) has found this to be a single, variable, and wide-ranging species reported under several names. He placed these taxa names in synonymy and noted that *C. flaccidum* is apparently the earliest validly published name for the species.

### *Ceramium nitens* (C. Agardh) J. Agardh

*Ceramium nitens* (C. Agardh) J. Agardh, 1851:130.—Taylor, 1960:535, pl. 66, fig. 14.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 1, 30 Mar 1976, JN-7262 and 25 Apr 1979, JN-7728; sta 3, 28 Apr 1977, JN-6396; sta 8, growing on a gorgonian, 4 Apr 1976, JN-6302. South Water Cay: sta 21, 29 Apr 1977, JN-6383, coll. O. McConnell; sta 22, epiphytic on *Sargassum* stipe, 28 Apr 1977, JN-6716.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Belize, Colombia (Taylor, 1960); Grand Cayman, St. Kitts, Dominica, Barbados (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Venezuela (Taylor, 1976).

### \* *Crouania attenuata* (Bonnemaison) J. Agardh

*Crouania attenuata* (Bonnemaison) J. Agardh, 1842:83.—Børgeisen, 1917:230, figs. 219–221.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, epiphytic on *Stylopodium*, 4 Apr 1976, JN-6306; sta 8, epiphytic on *Liagora pinnata*, 29 Mar 1976, JN-6212 (⊕), epiphytic on *Valonia ventricosa*, 27 Apr 1977, JN-6407 (♂), JN-6433 (♂), and JN-

6436a, and epiphytic on *Halimeda*, JN-6421a (♀); sta 9, epiphytic on *Sargassum* blade, 29 Apr 1977, JN-6838a (⊕); sta 10, epiphytic on *Galaxaura*, 23 Apr 1977, JN-6908 (⊕); sta 14, epiphytic on *Halimeda*, 27 Apr 1977, JN-6802 (♂).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Barbados (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Antigua (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b).

**REMARKS.**—This is the first report of this genus in Belize.

### \* *Griffithsia globulifera* (Harvey) J. Agardh

*Griffithsia globulifera* (Harvey) J. Agardh, 1876:67.—Børgeisen, 1917:202, figs. 191–193.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 2, on *Strombus gigas* (Queen conch) shell, 22 Apr 1977, JN-7225 (♂); sta 7, 22 Apr 1977, JN-6991a; sta 8, 27 Apr 1977, JN-6426 and JN-6432; sta 9, 29 Apr 1977, JN-6836; sta 10, epiphytic on *Galaxaura*, 23 Apr 1977, JN-6909.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Virgin Islands, Guadeloupe, Barbados, Venezuela (Taylor, 1960); Jamaica (Chapman, 1963); Puerto Rico (Almodóvar, 1964); Curaçao (van den Hoek, 1969).

**REMARKS.**—The two morphologically similar species, *Griffithsia globulifera* and *G. schousboei* Montagne are most easily separated by their spermatangium. The Belizean plant is assigned to *G. globulifera* (JN-7225), because it lacks the involucrum on the spermatangia, a feature ascribed to *G. schousboei* (Taylor, 1960). The spermatangia of the Carrie Bow Cay specimen are borne on terminal cells of the filaments as a cap, and in a ring about subterminal cells. Our specimens are the first record of the genus in Belize.

### \* *Anotrichium tenue* (C. Agardh) Naegeli

FIGURE 103

*Anotrichium tenue* (C. Agardh) Naegeli, 1861:399.—Børgeisen,



FIGURE 103.—*Anotrichium tenuis*, upper portion of axes showing tetrasporangia borne terminally on pedicels (JN-6926).

1920:462, fig. 423 [as *Griffithsia tenuis*].—Taylor, 1960:516 [as *Griffithsia tenuis*].—Baldock, 1976:556, figs. 49–64.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, intermixed in an algal turf, with *Jania* and *Ceramium*, 22 Apr 1977, JN-6958 (⊕); sta 8, 27 Apr 1977, JN-6434 (⊕); sta 10, epiphytic on *Dictyota*, 23 Apr 1977, JN-6925 (⊕).

**CARIBBEAN DISTRIBUTION.**—Hispaniola, Virgin Islands, Barbados (Taylor, 1960); Cuba (Suarez, 1973); Jamaica (Chapman, 1963); Puerto Rico (Almodóvar and Blomquist, 1965); St. Lucia

(Taylor, 1969); Costa Rica (Dawson, 1962b); Curaçao (van den Hoek, 1969).

**REMARKS.**—Baldock (1976:550, figs. 60, 61) described and illustrated Australian specimens of *Anotrichium tenuis*, in which the tetrasporangia were borne subterminally on pedicels; he suggested the position of the tetrasporangia be compared to material from other regions. Our specimens, a new record of the genus from Belize, bear mature and developing tetrasporangia terminally (Figure 103). They also differ from Australian *A. tenuis* by having fewer tetrasporangia per whorl. Belizean

plants have commonly 4–9, while specimens from Hong Kong (Tseng, 1942) and Australia (Baldock, 1976) have 8–10 (–12) tetrasporangia per whorl. Before placing taxonomic significance on these differences it will be necessary to study variation of tetrasporangial position within plant populations. It is also important to examine the tetrasporangia in the type of *Griffithsia tenuis* C. Agardh (1928) and in additional material from the type locality.

\* *Seirospora occidentalis* Børgesen

FIGURE 104

*Seirospora occidentalis* Børgesen, 1909:14; 1917:222, figs. 209–212.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 9, 29 Apr 1977, JN-6850a (♀); sta 15, epiphytic on *Dictyota*, 5 Apr 1976, JN-6341 (♀), and epiphytic on *Sargassum*, JN-6348 (seirospores), and 27 Apr 1977, epiphytic on *Sargassum* blade, JN-6692 (♀) and JN-6693b (♂).

CARIBBEAN DISTRIBUTION.—Bahamas, Virgin Islands, Guadeloupe (Taylor, 1960); Puerto Rico (Almodóvar and Blomquist, 1965).

REMARKS.—Carposporangial, spermatangial, and thalli with the distinctive seirospores in chains (Børgesen, 1909, 1917) were found in the Carrie Bow Cay specimens. They represent a new Belizean record for the genus.

\* *Spermothamnion investiens*  
(P. and H. Crouan) Vickers and Shaw

*Spermothamnion investiens* (P. and H. Crouan in Mazé and Schramm) Vickers and Shaw, 1905:64.—Børgesen, 1917: 200, figs. 189, 190.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 9, 29 Apr 1977, JN-6847; sta 18, epiphytic on *Galaxaura*, 25 Apr 1977, JN-6758a (⊕).

CARIBBEAN DISTRIBUTION.—Bahamas, Virgin Islands, Guadeloupe, Barbados (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); Curaçao (Diaz-Piferrer, 1964a). This is a new Belizean record for the genus.

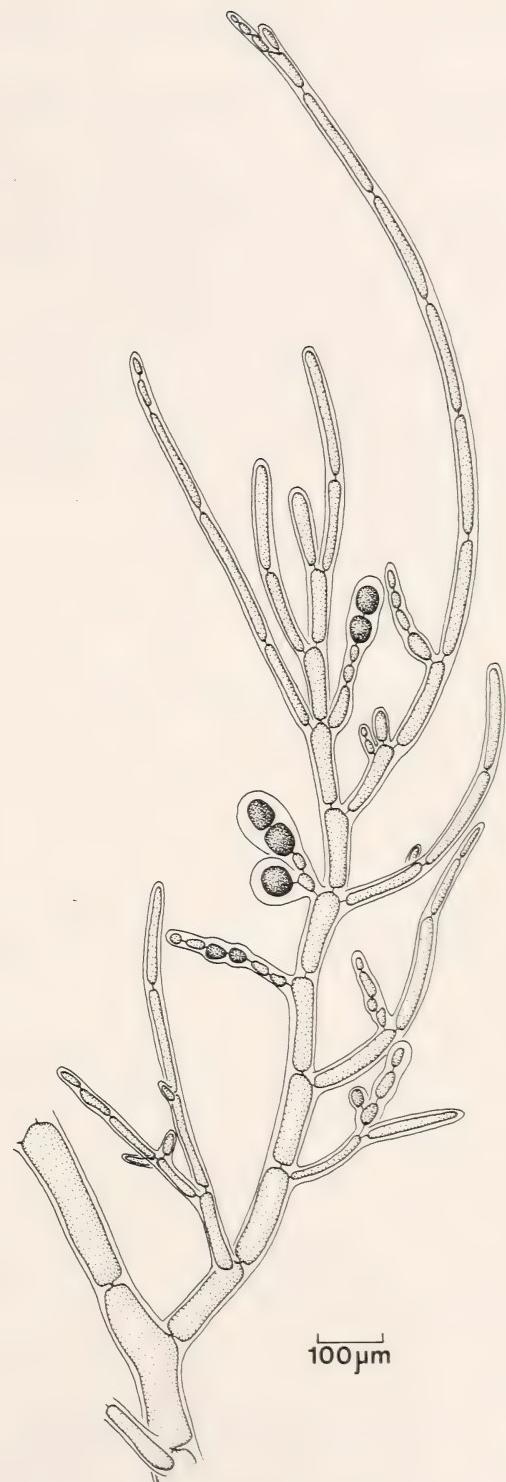


FIGURE 104.—*Seirospora occidentalis*, a small portion of the thallus showing the characteristic seirospores in chains (JN-6348).

### ***Spyridia filamentosa* (Wulfen) Harvey ex Hooker**

*Spyridia filamentosa* (Wulfen) Harvey ex Hooker, 1833:337.—Børgesen, 1917:233, fig. 222–226.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, 31 Mar 1976, JN-6274 (⊕), and 29 Apr 1979, JN-7394 and JN-7397; sta 25, 26 Apr 1977, JN-6866 (♀); sta 26, 22 Apr 1979, JN-7439 (♂).

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, St. Eustatius, Guadeloupe, Martinique, Barbados, Grenada, Belize, Costa Rica, Panama, Colombia, Netherlands Antilles, Isla las Aves (Taylor, 1960); Antigua, St. Lucia (Taylor, 1969); Venezuela (Diaz-Piferrer, 1970b); Trinidad (Richardson, 1975).

### ***Wrangelia argus* Montagne**

*Wrangelia argus* Montagne, 1856:444.—Taylor, 1960:502, pl. 66: figs. 7–8.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6986 (⊕); sta 8, 27 Apr 1977, JN-6419 (⊕); sta 9, epiphytic on *Dictyota*, 29 Apr 1977, JN-6837; sta 18, 25 Apr 1977, JN-7226. South Water Cay: sta 21, 28 Apr 1977, JN-6731 (♀, ♂).

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Trinidad, Tobago (Taylor, 1960); Cuba (Suarez, 1973); Dominican Republic (Almodóvar and Bonnelly, 1977); St. Kitts, Nevis, Dominica, St. Lucia (Taylor, 1969); Belize (Tsuda and Dawes, 1974).

### \* ***Wrangelia penicillata* C. Agardh**

*Wrangelia penicillata* C. Agardh, 1828:138.—Taylor, 1960: 503, pl. 66: figs. 5–6, pl. 74: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, epiphytic on *Liagora farinosa*, 29 Mar 1976, JN-6162 (⊕), and epiphytic on *Caulerpa verticillata*, 27

Apr 1977, JN-6414 (⊕); sta 9, 29 Apr 1977, JN-6841a (♂).

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Jamaica, Virgin Islands, Guadeloupe (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Dominican Republic (Almodóvar and Bonnelly, 1977); Puerto Rico (Almodóvar, 1964); Grand Cayman, Nevis, Barbados (Taylor, 1969); Colombia (Schnetter and Bula Meyer, 1977); Curaçao (van den Hoek, 1969); Venezuela (Diaz-Piferrer, 1970b).

### **Family DELESSERIACEAE**

#### ***Caloglossa leprieurii* (Montagne) J. Agardh**

*Caloglossa leprieurii* (Montagne) J. Agardh, 1876:499.—Taylor, 1960: 544, pl. 68: fig. 1.

LOCAL DISTRIBUTION.—Twin Cays: sta 26, growing on mangrove roots, 22 Apr 1979, JN-7445.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Barbados, Belize, Panama, Colombia (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Grenada (Taylor, 1969); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Venezuela (Taylor, 1976); Trinidad (Richardson, 1975).

#### ***Martensia pavonia* (J. Agardh) J. Agardh**

*Martensia pavonia* (J. Agardh) J. Agardh, 1863:831.—Børge- sen, 1919:348, figs. 344–346.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 9, 29 Apr 1977, JN-6830; sta 11, 23 Apr 1979, JN-7688; sta 14, epiphytic on *Sargassum*, 5 Apr 1976, JN-6352.

CARIBBEAN DISTRIBUTION.—Mexico, Jamaica, Virgin Islands, Guadeloupe (Taylor, 1960); Cuba (Suarez, 1973); Puerto Rico (Almodóvar, 1964); Antigua, Barbados (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Venezuela (Diaz-Piferrer, 1970b).

#### \* ***Taenioma nanum* (Kützing) Papenfuss**

*Taenioma nanum* (Kützing) Papenfuss, 1952:179.—Joly, 1965: 213, pl. 45: figs. 568, 569.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, in turf, 23 Jun 1977, coll. K. Rützler, CBC-77.6.23, and in turf with *Centroceras* and *Herposiphonia*, 22 Apr 1977, JN-6989b; sta 18, on *Dictyota*, 25 Apr 1977, JN-6751b.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Virgin Islands (Taylor, 1960, as *T. macrourum*); Cuba (Taylor, 1969); Curaçao (van den Hoek, 1969); Venezuela (Taylor, 1976).

**REMARKS.**—A small creeping species, it is found in the shallow-water turf community and represents a new generic record for Belize. Blades of specimen JN-6751b end mostly in two apical hairs, except for one that terminates in three hairs. All of its blades are 5 cells broad. Dawson (1962a:82–83), studying *Taenioma perpusillum* (J. Agardh) J. Agardh from Pacific Mexico, noted that their blades terminated in one, two or three hairs, “so that it is difficult to accept the number of terminal hairs as a basis for distinguishing these two species.” More recently, Ganesan and Lemus (1969) observed mostly two or sometimes only one, but never three hairs in *T. nanum* from Venezuela. Clearly, critical studies are needed to evaluate the status of these two taxa.

#### \* *Nitophyllum* species

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 18, 25 Apr 1977, JN-7170(⊕).

**REMARKS.**—Small monostromatic blades, with entire margins, 1 cm tall, are tentatively referred to this genus. Only tetrasporangial thalli were found. Tetrasporangial sori are round to oblong, 300 µm to 1000 µm in diameter, and located near the blade margins. This material may represent a new species but more specimens, particularly cystocarpic ones, are needed before its generic and specific placement can be determined. Similar specimens from St. Croix, U.S. Virgin Islands (J. L. Connor, pers. comm.) contain tetrasporic and cystocarpic thalli. The tetrasporangial thalli are undistinguishable from those from Belize. The cystocarps of the St. Croix specimen have carpospores borne terminally on gonioblast filaments, a characteristic of the genus *Nitophyllum*, which separates it from the morphologically similar *Myriogramme*.

#### \* *Hypoglossum tenuifolium* var. *carolinianum* Williams

*Hypoglossum tenuifolium* var. *carolinianum* Williams in Pearse and Williams, 1951:156 [as ‘*caroliniana*’].—Williams 1948: 693, figs. 12–17, [as *H. tenuifolium*].—Taylor, 1960:546.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 8, 27 Apr 1977, JN-6418 (⊕), and on *Valonia macrophysa*, JN-6409; sta 10, 23 Apr 1977, JN-7213; sta 14, 27 Apr 1977, JN-6801 (♀).

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Jamaica, Virgin Islands, Guadeloupe, Netherlands Antilles, Venezuela (Taylor, 1960).

**REMARKS.**—This is the first report of the genus in Belize.

#### Family DASYACEAE

##### \* *Dasya rigidula* (Kützing) Ardisson

*Dasya rigidula* (Kützing) Ardisson, 1878:140.—Taylor, 1960: 558, pl. 72: fig. 4.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, entangled in *Spyridia filamentosa*, 31 Mar 1976, JN-6275; sta 25, 26 Apr 1977, JN-6885 (⊕) and JN-6874.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Cayman Islands, Jamaica, Venezuela (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Antigua, St. Lucia (Taylor, 1969); Curaçao (van den Hoek, 1969).

**REMARKS.**—It represents a new Belizean record of the genus.

##### \* *Dasyopsis antillarum* Howe

###### FIGURE 105

*Dasyopsis antillarum* Howe, 1920b:577.—Taylor, 1960:564.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 8, 27 Apr 1977, JN-6697 (⊕), and JN-7044 (⊕); sta 14, epiphytic on *Styropodium zonale*, 5 Apr 1976, JN-6337.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba (Taylor, 1960); Venezuela (Diaz-Piferrer, 1970b).

**REMARKS.**—This is a new Belizean record for the genus.

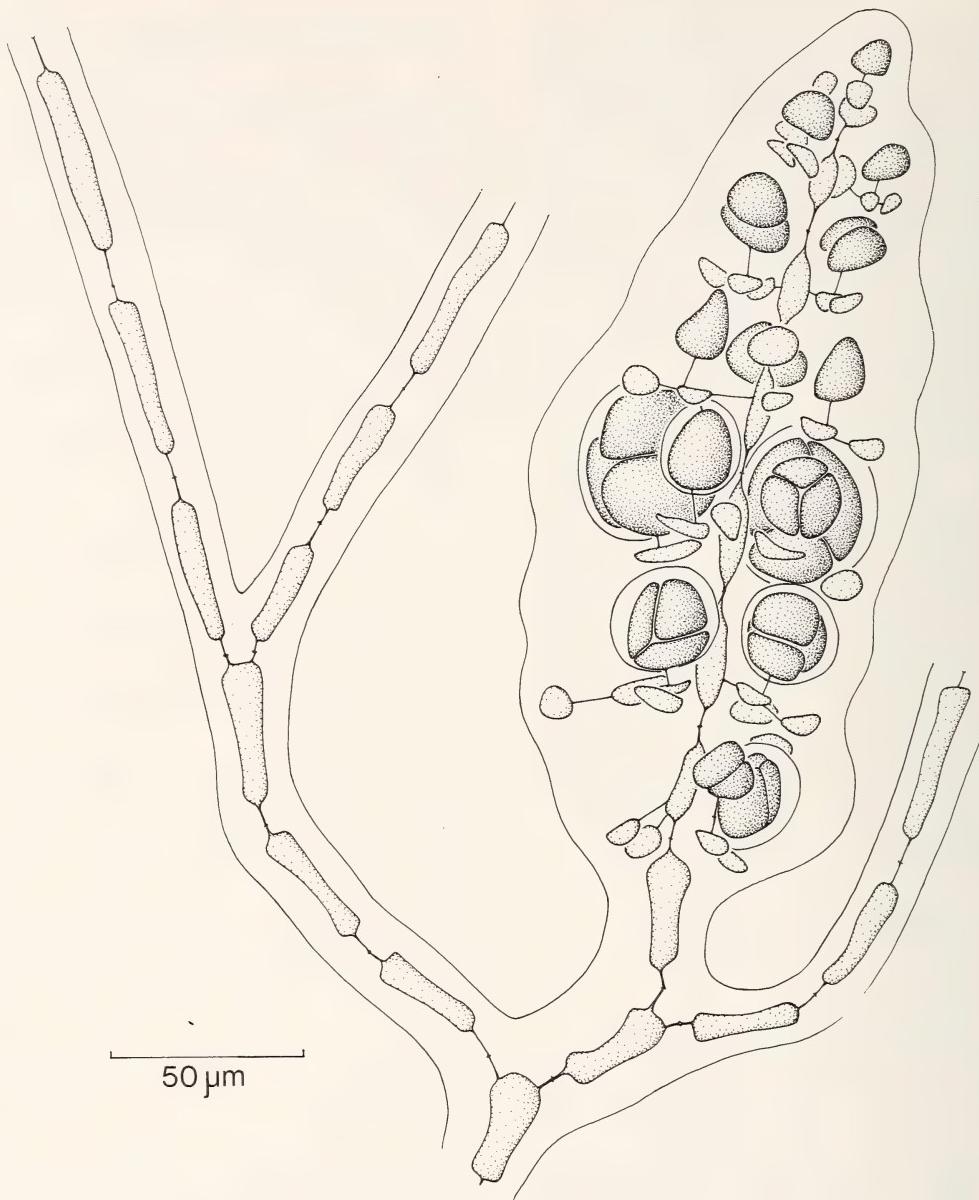


FIGURE 105.—*Dasyopsis antillarum*, portion of the thallus with tetrasporangial stichidia and some vegetative filaments (JN-7044).

\* ***Halodictyon mirabile* Zanardini**

*Halodictyon mirabile* Zanardini, 1843:52.—Taylor, 1960:567, pl. 72: fig. 5.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, epiphytic on *Stylopodium zonale*, 4 Apr 1976, JN-6304, and on *Caulerpa verticillata*, 27 Apr 1977, JN-6416 and JN-6436b; sta 9, on *Sargassum*, 29 Mar

1976, JN-6171, and on *Dictyota*, 23 Apr 1977, JN-7211; sta 10, on *Halimeda*, 25 Apr 1977, JN-7219.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica, Barbados (Taylor, 1960); Curaçao (van den Hoek, 1969).

REMARKS.—Several nonreproductive specimens of this net-forming alga were discovered growing epiphytically on larger algae. These rep-

resent a new Belizean record for the genus.

\* ***Heterosiphonia wurdemanni* var. *laxa***  
Børgesen

*Heterosiphonia wurdemanni* var. *laxa* Børgesen, 1919:326, figs. 327, 328.—Taylor, 1960:565, pl. 72: fig. 9.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 26, 29 Apr 1979, epiphytic on *Caulerpa paspaloides*, JN-7286 (⊕), JN-7287 (⊕), JN-7288 (⊕), and JN-7421 (⊕), and epiphytic on *Acanthophora spicifera*, JN-7425.

**CARIBBEAN DISTRIBUTION.**—Hispaniola (Taylor and Arndt, 1929); Virgin Islands (Børgesen, 1919).

**REMARKS.**—Morphologically this species is very similar to *Dasya rigidula*. However, the base of the monosiphonous laterals in *Heterosiphonia* is often polysiphonous, whereas the basal cell of the monosiphonous filaments in *Dasya* is always a single cell.

**Family RHODOMELACEAE**

***Acanthophora spicifera* (Vahl) Børgesen**

*Acanthophora spicifera* (Vahl) Børgesen, 1910:201.—Taylor, 1960:620, pl. 71: fig. 3; pl. 72: figs. 1, 2.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 2, 27 Apr 1979, JN-7636; on pebble on sandy beach, 29 Jun 1972, coll. F.R. Fosberg-54442, and D. Spellman. South Water Cay: sta 23, 29 Apr 1979, JN-7542. Twin Cays: sta 24, 31 Mar 1976, JN-6270; sta 25, 26 Apr 1977, JN-6878, and 29 Apr 1979, JN-7583; sta 26, 29 Apr 1979, JN-7283.

**CARIBBEAN DISTRIBUTION.**—Mexico, Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Dominica, Martinique, Barbados, Grenada, Guatemala, Old Providence Island, Costa Rica, Panama, Colombia, Netherlands Antilles, Isla las Aves, Venezuela, Trinidad, Tobago (Taylor, 1960); Grand Cayman, Nevis, Antigua, St. Lucia, Bequia (Taylor, 1969); Belize (Tsuda and Dawes, 1974).

**REMARKS.**—This plant is widely distributed throughout the Caribbean Sea, and the Atlantic,

Pacific, and Indian oceans (Cordeiro-Marino, 1978). In Belize it is common and forms dense expanding clumps.

\* ***Bostrychia binderi* Harvey**

*Bostrychia binderi* Harvey, 1849:68.—Taylor, 1960:598.—Cordeiro-Marino, 1978:120, figs. 356–359.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, growing on mangrove roots, 31 Mar 1976, JN-6293b, and 26 Apr 1977, JN-6871 and JN-6888a.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Hispaniola, Virgin Islands, Tortola Island, Guadeloupe, Martinique, St. Vincent, Barbados, Panama, Venezuela, Trinidad (Taylor, 1960); Puerto Rico (Diaz-Piferrer, 1963); St. Kitts, Antigua (Taylor, 1969); Curaçao (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b).

**REMARKS.**—This species is also known from other parts of the tropical western Atlantic, and from the tropical Pacific and Indian Oceans (Cordeiro-Marino, 1978).

***Bostrychia montagnei* Harvey**

*Bostrychia montagnei* Harvey, 1853:55.—Taylor, 1960:598, pl. 74: fig. 1.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, 31 Mar 1976, JN-6293a.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Jamaica, Belize (Taylor, 1960).

***Bostrychia tenella* (Vahl) J. Agardh**

*Bostrychia tenella* (Vahl) J. Agardh, 1863:869.—Taylor, 1960: 599.—Cordeiro-Marino, 1978:121, figs. 360–363.

**LOCAL DISTRIBUTION.**—Twin Cays: sta 24, entangled with *Catenella*, 31 Mar 1976, JN-6279 ⊕.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Martinique, Barbados, Grenada, Belize, Costa Rica, Venezuela (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Antigua, Bequia (Taylor, 1969); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Trinidad (Richardson, 1975).

\* ***Chondria polyrhiza* Collins and Hervey**

*Chondria polyrhiza* Collins and Hervey, 1917:121, pl. 2: fig. 12.—Cordeiro-Marino, 1978:128, figs. 388–391.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 8, epiphytic on *Halimeda*, 29 Mar 1976, JN-6158, and epiphytic on *Sargassum*, JN-6174 (⊕); sta 10, epiphytic on *Dictyota*, 23 Apr 1977, JN-6027 (♀); sta 14, epiphytic on *Sargassum* blade, 27 Apr 1977, JN-6800 (⊕); sta 15, epiphytic on *Sargassum*, 5 Apr 1976, JN-6354.

CARIBBEAN DISTRIBUTION.—Mexico (Humm and Hildebrand, 1962); Bahamas, Virgin Islands, (Taylor, 1960); Puerto Rico (Almodóvar and Blomquist, 1965); Costa Rica (Dawson, 1962b); Curaçao (van den Hoek, 1969); Venezuela (Diaz-Piferrer, 1970b).

***Digenia simplex* (Wulfen) C. Agardh**

*Digenia simplex* (Wulfen) C. Agardh, 1822:389.—Taylor, 1960:589.—Woelkerling, 1976:126, figs. 203–205.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 3, cast ashore, 22 Apr 1979, JN-7823. South Water Cay: sta 23, 30 Apr 1979, JN-7321. Twin Cays: sta 25, 26 April 1977, JN-6894b.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Turks Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Martinique, Grenada, Belize, Panama (Taylor, 1960); Grand Cayman, St. Kitts, Nevis, Antigua, Dominica, St. Lucia, Bequia (Taylor, 1969); Barbados (Almodóvar and Pagan, 1967); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Costa Rica (Dawson, 1962b); Venezuela (Taylor, 1976).

\* ***Herposiphonia pecten-veneris* (Harvey)  
Falkenberg**

*Herposiphonia pecten-veneris* (Harvey) Falkenberg, 1901:315.—Taylor, 1960:603.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 5, 24 Apr 1977, JN-7220; sta 8, epiphytic on *Udotea*, 29 Mar 1976, JN-6156 (⊕); sta 9, epiphytic on *Sargassum*, 29 Apr 1977, JN-6844.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Jamaica (Taylor, 1960); Cuba (Suarez, 1973); Venezuela (Taylor, 1976).

REMARKS.—Børgesen (1920:470) thought this taxon could be a form of *Herposiphonia tenella*. Tseng (1944), while recognizing the species *H. pecten-veneris*, discussed its uncertain taxonomic relationship to *H. tenella* and noted that examination of cystocarpic and spermatangial thalli would help to resolve the problem. Unfortunately, we have not encountered either in our collections.

***Herposiphonia secunda* (C. Agardh) Ambronn**

*Herposiphonia secunda* (C. Agardh) Ambronn, 1880:197.—Taylor, 1960:604, pl. 72: figs. 10, 11.—Cordeiro-Marino, 1978:125, figs. 378–381.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, 21 Apr 1977, JN-6937a (⊕).

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Barbados, Grenada, Belize, Panama, Netherlands Antilles (Taylor, 1960); Puerto Rico (Almodóvar, 1965); Nevis, Antigua, Dominica (Taylor, 1969).

REMARKS.—Børgesen (1918:290, fig. 289) found branching patterns attributed to *Herposiphonia secunda* on otherwise typical *H. tenella* thalli and concluded that *H. secunda* was “most probably . . . nothing more than a reduced form or variety of *H. tenella*.” Hollenberg (1968b:556), after examining what was considered to be an isotype of *H. secunda*, shared the view that the branching pattern is variable and reduced the species to a form: *H. tenella* f. *secunda*. Børgesen (1920:469–474) later changed his earlier opinion and concluded the two taxa were separate species because they had “two very different types of antheridial plants.” Most subsequent authors have followed this view and recognized not only differences in branching pattern, but also in dimensions, spermatangial features, and number of pericentral cells (for example, Taylor, 1960; Dawson, 1963; Oliveira Filho, 1969; Cordeiro-Marino, 1978). We are adopting this approach until crit-

ical studies have evaluated the taxonomic importance of these features.

Our Belizean material has 7–8 pericentral cells and axes not exceeding 80  $\mu\text{m}$  in diameter. It is therefore closest in vegetative features to *Herposiphonia secunda* as described from elsewhere in the Caribbean (Taylor, 1960).

#### \* *Lophosiphonia cristata* Falkenberg

*Lophosiphonia cristata* Falkenberg, 1901:499.—Børgesen, 1918: 297, figs. 295–298.—Taylor, 1960:606.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-7128a.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica, Virgin Islands (Taylor, 1960); Cuba (Suarez, 1973); Puerto Rico (Diaz-Piferrer, 1963); Grand Cayman, Antigua (Taylor, 1969); Isla San Andrés (Kapraun, 1972); Curaçao (van den Hoek, 1969).

REMARKS.—It is the first record of the genus in Belize.

#### *Polysiphonia atlantica* Kapraun and Norris

*Polysiphonia atlantica* Kapraun and Norris, herein: 226, Figure 107a–c.—Børgesen, 1918:274, figs. 272–276 [as *P. macrocarpa* Harvey].

LOCAL DISTRIBUTION.—Twin Cays: sta 24, epiphytic on *Ulva*, 31 Mar 1976, JN-6292 ( $\oplus$ ).

CARIBBEAN DISTRIBUTION.—Virgin Islands, Barbados (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Jamaica (Chapman, 1963); Costa Rica (Dawson, 1962b); Belize (Kapraun and Norris, herein); Curaçao (Diaz-Piferrer, 1964b).

#### *Polysiphonia denudata* (Dillwyn) Greville ex Harvey

*Polysiphonia denudata* (Dillwyn) Greville ex Harvey in Hooker, 1833:332.—Taylor, 1960:580.—Kapraun and Norris, herein: 228, Figure 107d–f.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 10, epiphytic on *Dictyota*, 29 Apr 1977, JN-6842a ( $\oplus$ ); sta 15, 27 Apr 1977, JN-6805 ( $\varnothing$ ,  $\oplus$ ), and epiphytic on *Stylopodium zonale*, JN-6686 ( $\oplus$ ).

CARIBBEAN DISTRIBUTION.—Virgin Islands,

Guadeloupe, Barbados, Netherlands Antilles (Taylor, 1960); Cuba (Suarez, 1973); Belize (Kapraun and Norris, herein).

#### *Polysiphonia exilis* Harvey

*Polysiphonia exilis* Harvey, 1853:47.—Taylor, 1960:581.—Kapraun and Norris, herein: 228, Figure 108.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 15, epiphytic on *Dictyota dichotoma*, 5 Apr 1976, JN-6342a–c ( $\delta$ ).

CARIBBEAN DISTRIBUTION.—Bahamas (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Belize (Kapraun and Norris, herein); Curaçao (Diaz-Piferrer, 1964b).

#### *Polysiphonia ferulacea* Suhr

*Polysiphonia ferulacea* Suhr in J. Agardh, 1863:980.—Taylor, 1960:578.—Kapraun and Norris, herein: 229, Figure 109.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, entangled with *Jania*, *Centroceras*, and *Wrangelia* turf, JN-6987; sta 8, 27 Apr 1977, epiphytic on *Valonia ventricosa*, JN-6410 ( $\oplus$ ), and epiphytic on *Caulerpa verticillata*, JN-6413; sta 10, 23 Apr 1977, epiphytic on *Udotea*, JN-6938 ( $\delta$ ); sta 15, 5 Apr 1976, epiphytic on *Dictyota cervicornis*, JN-6334 ( $\varnothing$ ), JN-6335 ( $\varnothing$ ), and epiphytic on *Lobophora variegata*, JN-6355 ( $\oplus$ ), and 27 Apr 1977, JN-6691b.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Barbados, Costa Rica, Venezuela (Taylor, 1960); Cuba (Diaz-Piferrer, 1964a); Puerto Rico (Almodóvar and Blomquist, 1965); St. Kitts, Antigua, Dominica (Taylor, 1969); Belize (Kapraun and Norris, herein); Curaçao (Diaz-Piferrer, 1964b); Trinidad (Richardson, 1975).

#### *Polysiphonia flaccidissima* Hollenberg

*Polysiphonia flaccidissima* Hollenberg, 1942:783.—Hollenberg and Norris, 1977:4, fig. 2E.—Kapraun and Norris, herein: 231, Figure 110.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 10,

epiphytic on *Dictyota*, 29 Apr 1977, JN-6842b ( $\oplus$ , ♀, ♂); sta 15, epiphytic on *Sargassum hystrix*, 5 Apr 1976, JN-6351 ( $\delta$ , ♀), JN-6353 ( $\oplus$ ). Twin Cays: sta 24, epiphytic on *Anadyomene stellata*, 26 Apr 1977, JN-6886 (♀,  $\oplus$ ).

CARIBBEAN DISTRIBUTION.—Belize (Kapraun and Norris, herein).

***Polysiphonia scopulorum* var. *villum*  
(J. Agardh) Hollenberg**

*Polysiphonia scopulorum* var. *villum* (J. Agardh) Hollenberg, 1968a:81.—Hollenberg and Norris, 1977:14, fig. 8B.—Kapraun and Norris, herein: 233, Figure 111.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 15, epiphytic on *Lobophora variegata*, 5 Apr 1976, JN-6357 (♀).

CARIBBEAN DISTRIBUTION.—Belize (Kapraun and Norris, herein).

***Polysiphonia sphaerocarpa* Børgesen**

*Polysiphonia sphaerocarpa* Børgesen, 1918:271.—Taylor, 1960: 576.—Kapraun and Norris, herein: 233, Figure 112.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 10, 29 Apr 1977, epiphytic on *Sargassum*, JN-6847a, and 23 Apr 1977, epiphytic on *Dictyota*, JN-6911 (♀); sta 18, epiphytic on *Dictyota*, JN-6746 (♀), JN-6747b (♂), JN-6748 ( $\oplus$ ), and JN-6755 (♀,  $\oplus$ ).

CARIBBEAN DISTRIBUTION.—Hispaniola, Virgin Islands (Taylor, 1960); Antigua, Dominica, Barbados (Taylor, 1969); Belize (Kapraun and Norris, herein).

***Murrayella periclados* (C. Agardh) Schmitz**

*Murrayella periclados* (C. Agardh) Schmitz, 1893:227.—Børgesen, 1919:314, figs. 318–320.—Taylor, 1960:593.

LOCAL DISTRIBUTION.—Twin Cays: sta 24, 29 Apr 1979, JN-7395 ( $\oplus$ ).

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Cayman Islands, Jamaica, Virgin Islands, Guadeloupe, Martinique, Barbados, Grenada, Belize, Guatemala, Panama, Venezuela (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Antigua (Taylor, 1969); Curaçao, Bonaire (Diaz-Piferrer, 1964b);

Trinidad (Richardson, 1975).

**\* *Laurencia caraibica* Silva**

*Laurencia caraibica* Silva, 1972:205.—Taylor, 1960:622 [as *Laurencia nana*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 22 Apr 1977, JN-6997. South Water Cay: sta 21, 29 Apr 1977, JN-6388.

CARIBBEAN DISTRIBUTION.—Bahamas, Jamaica (Taylor, 1960); Antigua (Taylor, 1969).

REMARKS.—The name *Laurencia caraibica* was introduced by Silva (1972) to replace *L. nana* Howe in Britton and Millspaugh (Howe, 1920b: 566), a later homonym of *L. nana* (C. Agardh) Greville (1830:1ii).

The plants from Belize are pink to light rose and form small decumbent clumps in shallow, wave-exposed portions of the reef crest. Lenticular thickenings occur in a few cell walls of the medulla and can be seen in both fresh and dried Carrie Bow Cay material. These were noted neither by Howe (1920b) nor by Yamada (1931) but re-examination of an isotype (US-68437, Howe 5393) has revealed their presence.

***Laurencia intricata* Lamouroux**

*Laurencia intricata* Lamouroux, 1813:43.—Børgesen, 1918: 251, figs. 241–242 [as *L. implicata*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 4, 25 Apr 1979, JN-7722; sta 19, 28 Apr 1979, JN-7627. Twin Cays: sta 24, 29 Apr 1979, JN-7393.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, Guadeloupe, Grenada, Costa Rica, Panama (Taylor, 1960); St. Kitts, Dominica, Bequia (Taylor, 1979); Belize (Tsuda and Dawes, 1974); Curaçao, Bonaire (Diaz-Piferrer, 1964b); Venezuela (Diaz-Piferrer, 1970b).

**\* *Laurencia microcladia* Kützing**

*Laurencia microcladia* Kützing, 1865:22, pl. 60: figs. b, c.—Cordeiro-Marino, 1978:130, figs. 395–396.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 2, 27 Apr 1979, JN-7644.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Barbuda, Guadeloupe, Isla las Aves, Costa Rica, Panama, Netherlands Antilles, Venezuela (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Nevis, Antigua, St. Lucia (Taylor, 1969); Dominica (Taylor and Rhyne, 1970).

### **Laurencia obtusa (Hudson) Lamouroux**

*Laurencia obtusa* (Hudson) Lamouroux, 1813:42.—Børgesen, 1918:247, figs. 237–240.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 21 Apr 1977, JN-6978, 22 Apr 1977, JN-6951 and JN-6961, 23 Apr 1976, JN-7667, and 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7487. South Water Cay: sta 21, 28 Apr 1977, JN-6728 and JN-6734.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Virgin Islands, St. Barthélemy, Guadeloupe, Barbados, Belize, Panama, Colombia, Netherlands Antilles, Isla las Aves, Tobago (Taylor, 1960); Puerto Rico (Almodóvar, 1964); Antigua, Dominica, St. Lucia (Taylor, 1969); Costa Rica (Dawson, 1962b); Venezuela (Taylor, 1976).

### **Laurencia papillosa (Forsskål) Greville**

*Laurencia papillosa* (Forsskål) Greville, 1830:1ii.—Taylor, 1960:623, pl. 74: fig. 2.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 28 Apr 1979, coll. J. Norris and I. Macintyre, JN-7486. South Water Cay: sta 21, 28 Apr 1977, JN-6720. Twin Cays: sta 24, 29 Apr 1979, JN-7392; sta 25, 26 Apr 1977, JN-6879.

CARIBBEAN DISTRIBUTION.—Mexico, Bahamas, Caicos Islands, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, St. Barthélemy, Guadeloupe, Barbados, Grenada, Belize, Costa Rica, Panama, Colombia, Netherlands Antilles, Venezuela, Trinidad (Taylor, 1960); St. Kitts, Nevis, Antigua, Dominica, St. Lucia, Be-

quia (Taylor, 1969); Isla San Andrés (Kapraun, 1972).

### \* ***Wrightiella blodgettii* (Harvey) Schmitz**

#### FIGURE 106

*Wrightiella blodgettii* (Harvey) Schmitz, 1893:221.—Taylor, 1960:591.

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 1, on lower side of *Diploria* sp., 20 Apr 1977, JN-7046 ⊕; sta 11, 25 Apr 1977, JN-7055.

CARIBBEAN DISTRIBUTION.—Bahamas, Guadeloupe (Taylor, 1960).

REMARKS.—The genus has distinctive spine-like or “spur” branchlets, monosiphonous laterals, and spiral tetrasporangial stichidia. Taxonomists have questioned whether *Wrightiella blodgettii* is distinct from *W. tumanowiczii* (Gatty) Schmitz (for instance, Børgesen, 1915; Schneider, 1975). The plants from Belize representing a new Belizean record for the genus, have numerous spur branchlets and are densely beset with monosiphonous branchlets; therefore, they agree with *W. blodgettii* as described by Taylor (1960).

This species is rare in the Carrie Bow Cay area. We found it on a patch reef and noted that it superficially resembled a small gorgonian.

### Order (incertae sedis)

#### Family WURDEMANNIACEAE

### ***Wurdemannia miniata* (Lamouroux) Feldmann and Hamel**

*Wurdemannia miniata* (Lamouroux) Feldmann and Hamel, 1934:544.—Børgesen, 1919:368, figs. 360–361 [as *Wurdemannia sectacea*].

LOCAL DISTRIBUTION.—Carrie Bow Cay: sta 7, 23 Apr 1979, JN-7678.

CARIBBEAN DISTRIBUTION.—Bahamas, Cuba, Jamaica, Virgin Islands, Guadeloupe, Isla las Aves (Taylor, 1960); Puerto Rico (Díaz-Piferrer, 1963); Dominica, Barbados (Taylor, 1969); Belize (Tsuda and Dawes, 1974); Curaçao, Bonaire

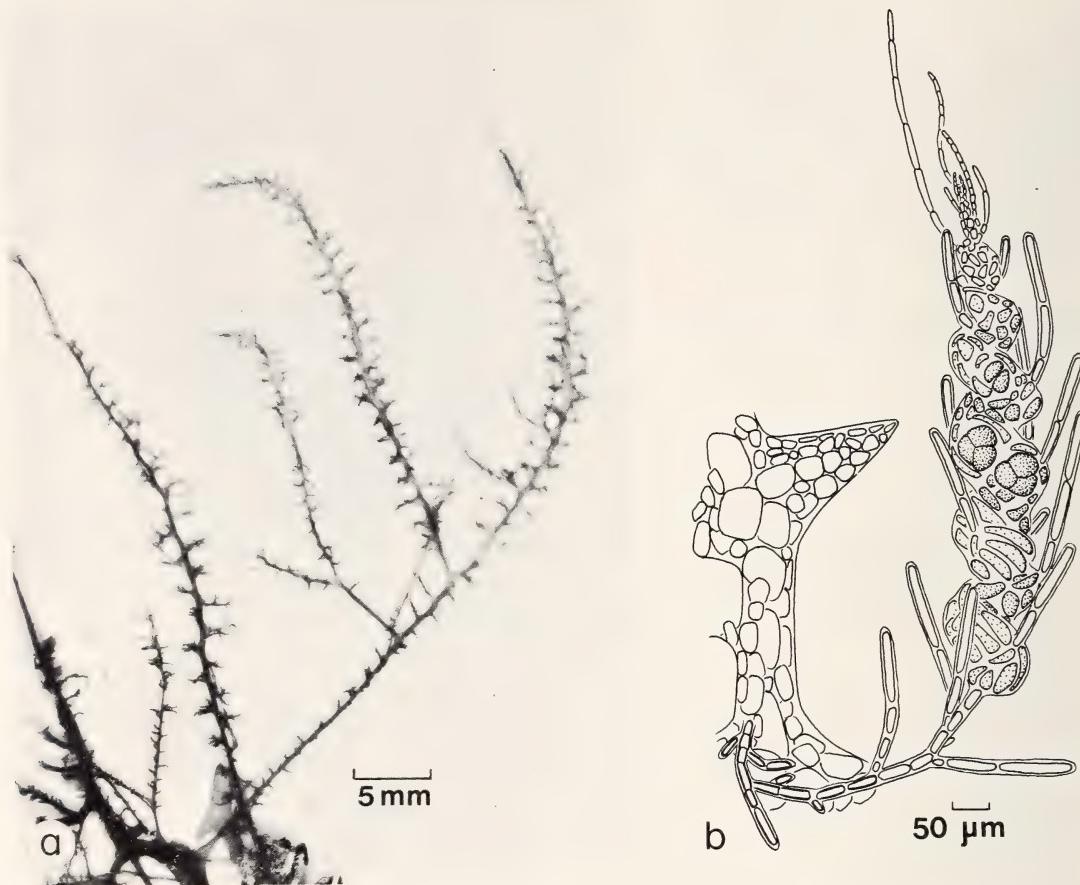


FIGURE 106.—*Wrightiella blodgettii* (JN-7046): *a*, portion of the thallus showing branches with numerous spur branchlets; *b*, portion of main axis with a spiral tetrasporangial stichidia.

(Diaz-Piferrer, 1964b); Panama (Earle, 1972); Venezuela (Taylor, 1976).

#### Division MAGNOLIOPHYTA (= ANGIOSPERMAE)

#### Class LILIOPSIDA (= MONOCOTYLEDONEAE)

#### Order NAJADALES

#### Family CYMODOCEACEAE

#### *Halodule wrightii* Ascherson

*Halodule wrightii* Ascherson, 1868:19.—den Hartog, 1970: 154.—Hanlon and Voss, 1975:18, fig. 4.—Howard, 1979: 11, fig. 3b-c.

LOCAL DISTRIBUTION.—South Water Cay: sta

21, 16 Nov 1980, JN-9818. Twin Cays: SW of sta  
26, 25 May 1980, coll. K. Rützler, JN-9815.

CARIBBEAN DISTRIBUTION.—Cuba, Haiti, Puerto Rico, Jamaica, St. Martin, Guadeloupe (den Hartog, 1970); Belize (Tsuda and Dawes, 1974).

#### *Syringodium filiforme* Kützing

*Syringodium filiforme* Kützing in Hohenacker, 1860: no. 426.—den Hartog, 1970:183.—Hanlon and Voss, 1975:20, figs. 5, 9.—Howard, 1979:12, fig. 3a.

LOCAL DISTRIBUTION.—South Water Cay: sta 21, 28 Apr 1977, JN-6733.

CARIBBEAN DISTRIBUTION.—Bahamas, Caicos, Cuba, Hispaniola, Puerto Rico, Jamaica, Cay-

man Islands, Virgin Islands, St. Martin, Antigua, Saba Island, Guadeloupe, Dominica, Martinique, Costa Rica, Panama, Isla de San Andrés, Curaçao, Tortuga Island (den Hartog, 1970); Belize (Tsuda and Dawes, 1974).

**REMARKS.**—Rather common and usually intermixed with *Thalassia* in sandy areas. Flowers were observed in April 1979.

## Order HYDROCHARITALES

### Family HYDROCHARITACEAE

#### ***Thalassia testudinum* Banks ex König**

*Thalassia testudinum* Banks ex König, 1805:96.—den Hartog, 1970:223.—Hanlon and Voss, 1975:12, figs. 1, 8.—Howard, 1979:24, Fig. 7a.

**LOCAL DISTRIBUTION.**—Carrie Bow Cay: sta 7, 23 Jun 1977, leg. K. Rützler, CBC-77.6.23. Twin Cays: sta 25, 26 Apr 1977, JN-6869.

**CARIBBEAN DISTRIBUTION.**—Bahamas, Cuba, Cayman Islands, Jamaica, Haiti, Puerto Rico, Virgin Islands, St. Barthélemy, Antigua, Guadeloupe, Martinique, Barbados, Grenada, Trinidad, Tortuga Island, Curaçao, Belize, Costa Rica, Panama (den Hartog, 1970).

**REMARKS.**—Widespread in the vicinity of Carrie Bow Cay, preferring sandy areas of the shallower depths. Flowers were observed in April 1979. Blades were often heavily laden with epiphytes in spring.

## Summary and Conclusions

Our collections of marine algae and seagrasses from the vicinity of Carrie Bow Cay yielded 34 genera, 77 species, six varieties, and five forms that are new to Belize. Thus, the marine flora of Belize now totals 247 plant taxa, including nine Cyanophyta, 73 Chlorophyta, 32 Phaeophyta, 124 Rhodophyta, and four Magnoliophyta (= Angiospermae).

Most major habitats of the lagoon, reef crest, and fore reef are characterized by certain common algae. A particularly interesting feature of

the lagoon is the mangrove community of Twin Cays (stations 24–26). The intertidal stilt roots of the predominant red mangrove support three species of *Bostrychia*, along with *Catenella repens* and *Caloglossa leprieurii*, all known to be common associates of mangroves (see Taylor, 1960). Mud-banks of the subtidal zone are covered by extensive mats of *Caulerpa verticillata* laden with detritus, and submerged roots provide substrate to two other *Caulerpa* species, *C. paspaloides*—an unusually large form of this species—and *C. mexicana*. Two other algae are conspicuous because they are commonly found on dead or even decaying mangrove roots, *Acetabularia crenulata* and *Neomeris annulata*. In the *Thalassia* bed adjacent to the mangroves (station 26), *Penicillus dumentosus* and *Rhipocephalus phoenix* are predominant, accompanied by less common *Dictyosphaeria cavernosa*. The seagrass beds closer to Carrie Bow Cay (station 4) are composed of *Thalassia testudinum* and *Syringodium filiforme*. They abound with *Udotea flabellum*, *Halimeda incrassata*, and *Avrainvillea longicalvis*, along with some epiphytic species of *Dasya*. Both seagrasses were in flower during our surveys between March and May.

The shallow reef flat (station 6) seaward of Carrie Bow Cay is also dominated by a *Thalassia* community. Two conspicuous components are the coralline algae *Amphiroa fragillissima* and *Neogoniolithon strictum*, the latter forming unattached nodules. *Thalassia* blades provide substrate for a number of small epiphytic algae. One of these, *Champia parvula*, was particularly abundant during spring 1979 when it appeared as a conspicuous yellow coverage over the greater part of the reef flat (see also Rützler and Macintyre, herein: 9, Figures 6b, 7b).

Shallow back-reef areas were also examined near South Water Cay, one kilometer to the north of Carrie Bow Cay. Their most distinctive features are widespread dense stands of *Turbinaria turbinata* and *Sargassum polyceratum* off the north tip of the cay (station 23). Rather patchy in distribution but unique to the area is *Ochiodes secundiramea* growing in the shallows of the reef crest east of the island (station 21).

The wave-exposed intertidal reef crest off Car-

rie Bow Cay (station 7) has a rich and characteristic algal flora. The leeward coral rock is covered by extensive mats of *Caulerpa racemosa* and *Hali-meda opuntia*. *Laurencia obtusa* and *L. caraibica* are most noticeable on the exposed parts of the crest, whereas numerous but small tufts of *Wrangelia argus* are found in surge areas. The abundant crustose corallines include *Hydrolithon boergesenii* and *Porolithon pachydermum*. Also common are turfs formed mainly by *Acetabularia myriospora* and *Neomeris mucosa*. Less abundant but characteristic for the reef crest and not found elsewhere are *Liagora valida*, *Eucheuma echinocarpum*, *E. schrammii*, and *Gracilaria crassissima*.

On the fore reef, red algae of the genus *Liagora* characterize the spur and groove zone (stations 8-10) in 4-12 m depth. *Liagora farinosa* and *L. pinnata* predominate, along with two possibly un-

described species, one belonging to *Liagora*, the other one to the related genus *Trichogloeopsis*. *Dudresnaya crassa*, generally considered rare in the Caribbean, is also common in this zone in the spring. *Lobophora variegata*, *Stylopodium zonale*, and *Anadyomene stellata* are abundant on the outer ridge and down the fore-reef slope to 40 m depth. All three species are also found in shallow water, although there they are morphologically different. Less common but restricted to this deep-water habitat are *Galaxaura obtusa* and *Kallymenia limminghii*.

Collecting during different seasons and in the diverse marine environments throughout the entire barrier reef, numerous cays, and along the mainland coast would be expected to result in the discovery of many plants as yet unknown or unreported in Belize.

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# The Red Alga *Polysiphonia* Greville (Rhodomelaceae) from Carrie Bow Cay and Vicinity, Belize

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## ABSTRACT

Seven taxa of the red alga *Polysiphonia* Greville (Rhodomelaceae; Ceramiales) were found near Carrie Bow Cay and Twin Cays in the central region of the Belizean barrier reef. *Polysiphonia exilis* and *P. flaccidissima* are new records for the Caribbean marine flora, *P. atlantica*, *P. denudata*, *P. ferulacea*, *P. scopulorum* var. *villum*, and *P. sphaerocarpa* are new to Belize. *Polysiphonia atlantica* is given as a new name for the preoccupied name *P. macrocarpa* Harvey. Most species occur as epiphytes on other algae, commonly on *Sargassum* and *Dictyota*. *Polysiphonia ferulacea* and *P. sphaerocarpa* are also found entangled in algal turfs, and *P. scopulorum* var. *villum* also occurs on mangrove roots.

## Introduction

Only two species of *Polysiphonia* Greville (1824) have been recorded previously from Belize (British Honduras): *P. havanensis* Montagne (Taylor, 1935; 1960) and *P. scopulorum* Harvey (Tsuda and Dawes, 1974). In our present study of *Polysiphonia* from Carrie Bow Cay and vicinity, we report six additional species and one variety new to the marine flora of Belize.

Several detailed studies of the taxonomy, distribution, and geographic variation of *Polysiphonia* have increased our knowledge of its members. In the Pacific Ocean, studies have covered the coasts of North America (Hollenberg, 1942, 1944), including Mexico (Hollenberg, 1961), and the northern Gulf of California (Hollenberg and Norris, 1977); Hawaii (Meñez, 1964); the central and western tropical Pacific (Hollenberg, 1968a, 1968b); southern Australia (Womersley, 1979); and Japan (Segi, 1951). In the Atlantic Ocean, work has focused on the coasts of North Carolina and Texas (Kapraun, 1977, 1979); Brazil (Oliveira Filho, 1969); Portugal (Ardré, 1970); and the western Mediterranean (Lauret, 1967, 1970).

We relied mainly on the following morphological features in distinguishing the taxa of *Polysiphonia*: number of pericentral cells; presence or absence of cortication; kind and position of origin of the attachment rhizoids; nature and position of trichoblasts; and nature of the spermatangial branchlets. Material for this study was collected from intertidal and subtidal habitats near Carrie Bow Cay and Twin Cays. These habitats are described and illustrated by Rützler and Macintyre (herein: 9), Rützler and Ferraris (herein: 77) and Norris and Bucher (herein: 167). Specimens, which were obtained by J. Norris (March-April, 1976), J. Norris and K. Bucher (April 1977), and D. Kapraun (March 1978), were mainly epiphytic on other algae. Collections are designated as follows: DK for D. F. Kapraun, JN

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for J. N. Norris, and KB for K. E. Bucher. The prefix initials of the numbers cited correspond to the collector's field notebooks. Reproductive condition is designated by  $\oplus$  for tetrasporangia, ♀ for cystocarps, and ♂ for spermatangia. Specimens studied are deposited in the Algal Collection, United States National Herbarium, Smithsonian Institution (US).

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### Key to the Species of *Polysiphonia* from Carrie Bow Cay and Vicinity

1. Pericentral cells 4 (subgenus *Oligosiphonia*) ..... 2  
Pericentral cells 5 or more (subgenus *Polysiphonia*) ..... 6
2. Branches arising in the axes of trichoblasts ..... *P. flaccidissima*  
Branches developmentally replacing trichoblasts ..... 3
3. Rhizoids in open connection with pericentral cells ..... 4  
Rhizoids cut off from pericentral cells ..... 5
4. Scar cells common in decumbent axes; trichoblasts in erect filaments branched 1–2 times ..... *P. atlantica*  
Scar cells absent in decumbent axes; trichoblasts in erect filaments highly branched to several orders ..... *P. scopulorum* var. *villum*
5. Plants small, to 1.5 cm tall, and delicate, main filaments less than 100  $\mu\text{m}$  in diameter; often epiphytic, erect filaments arising from a rhizoidal disc ..... *P. sphaerocarpa*  
Plants larger, to 4 cm tall, and coarse, decumbent axes to 250  $\mu\text{m}$  in diameter; erect filaments from entangled decumbent branches ..... *P. ferulacea*
6. Pericentral cells 5 (–6) ..... *P. denudata*  
Pericentral cells 8 ..... *P. exilis*

#### *Polysiphonia atlantica*, new name

FIGURES 107a–c

*Polysiphonia macrocarpa* Harvey in Mackay, 1836:206 [non *Polysiphonia macrocarpa* (C. Agardh) Sprengel 1827:350].—Collins and Hervey, 1917:123.—Børgesen, 1918:274, figs. 272–276.—Taylor, 1928:184; 1960:578.—Oliveira Filho, 1977:153.—Kapraun, 1977:317, figs. 14–21, 57; 1979:107, figs. 10–12.

**DESCRIPTION.**—Thalli minute, forming entangled mats to 1 cm tall; erect filaments sparsely subdichotomously branched; branches replacing trichoblasts in development; pericentral cells 4; erect filaments arising in unilateral fashion from prostrate axes; rhizoids remaining in open connection with pericentral cells. Tetrasporangia in long straight series in the branch tips.

**TYPE-LOCALITY.**—Portstewart; Miltown Malbay, Ireland.

**DISTRIBUTION.**—Tropical western Atlantic (Virgin Islands, Barbados, Curaçao, Costa Rica, Cuba, Jamaica); temperate eastern Atlantic; Indian Ocean.

**SPECIMENS STUDIED.**—Twin Cays: JN-6292 ( $\oplus$ ), epiphytic on *Ulva*, 1 m depth, among mangroves on E side of eastern half of Twin Cays, 31 Mar 1976.

**REMARKS.**—Reluctantly we abandon the name *Polysiphonia macrocarpa* Harvey, because it has been widely applied to this neotropical species. Recently, Womersley (1979:471) noted that *P. macrocarpa* Harvey in Mackay (1836) is a later hom-

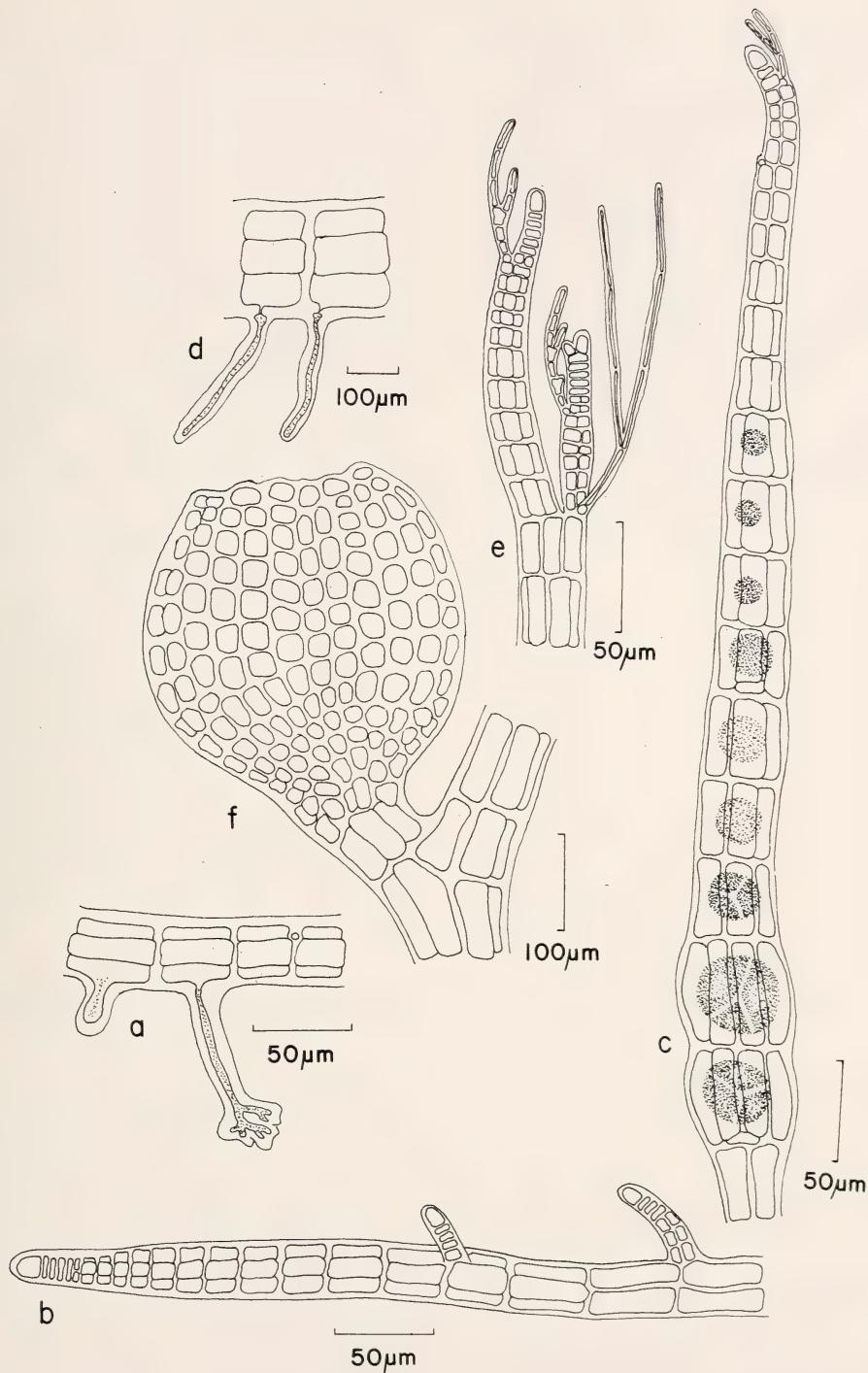


FIGURE 107.—*Polysiphonia atlantica*: a, rhizoids in open connection with pericentral cells (JN-6292); b, prostrate axis with unilateral development of erect filaments (JN-6292); c, tetrasporangia in long straight series (JN-6292). *Polysiphonia denudata*: d, rhizoids cut off at or near the end of pericentral cells (JN-6805); e, branch arising in axil of trichoblast (JN-6805); f, mature pericarp (JN-6805).

onym of *P. macrocarpa* (C. Agardh) Sprengel (1827:350) [basionym: *Hutchinsia macrocarpa* C. Agardh, 1824:157]. Pending further studies, we propose a new name, *P. atlantica* Kapraun and J. Norris, for Harvey's taxon. Parke and Dixon (1976:537) pointed out that this taxon is in need of taxonomic and nomenclatural re-investigation. In this treatment we follow Børgeesen (1918), Ardré (1970), and Kapraun (1977, 1979) in their interpretation of *P. macrocarpa* Harvey. Reported elsewhere in the Caribbean as *P. macrocarpa* (for instance, Taylor, 1960), the occurrence of this taxon in Belize is not surprising.

*Polysiphonia macrocarpa* (C. Agardh) Sprengel (1827) may well be an overlooked name for one of the several taxa described or reported in the Caribbean. *Hutchinsia macrocarpa* C. Agardh (1824) was originally described "In mari Antillarum, 'Port au Pray'." It is interesting that for other taxa in his *Systema algarum*, C. Agardh latinized localities, yet for *H. macrocarpa* he placed Port au Pray in quotation marks, leaving it in French form. By not using Latin for its locality, he may have wished to suggest something was wrong with the locality name. Could it be Port de Paix or Port au Prince (Haiti)? The type specimen (probably located at the Botanical Museum Lund) should be re-examined to determine the identity of this taxon, and compared to those taxa recorded from the Caribbean.

### ***Polysiphonia denudata* (Dillwyn) Greville ex Harvey**

FIGURE 107d-f

*Conferva denudata* Dillwyn 1809:85.

*Polysiphonia denudata* (Dillwyn) Greville ex Harvey in W. J. Hooker, 1833:332.

*Polysiphonia denudata* (Dillwyn) Kützing, 1849:824; 1863:28, pl. 90.—Taylor, 1960:580.—Joly, 1965:221, pl. 47: figs. 586–590.—Taylor and Bernatowicz, 1969:37.—Taylor, 1969:183.—Lauret, 1970:123, pl. 1: figs. 1–20, pl. 2: figs. 20–22.—Kapraun, 1977:321, figs. 38–42, 58; 1979:109, figs. 24–27.—Oliveira Filho, 1977:151.—Schnetter and Bula Meyer, 1977:89, fig. 17.

**DESCRIPTION.**—Thalli dark red, to 3 cm tall from a discoidal base; erect filaments dichotomously branched; branches widely divergent, be-

coming decumbent in older parts and attached to the substratum; rhizoids cut off at or near the end of pericentral cells; pericentral cells 5 (–6); branches arising in axils of trichoblasts. Pericarps spherical, 200–250 µm in diameter.

**TYPE-LOCALITY.**—Southhampton, England.

**DISTRIBUTION.**—Atlantic: North America, Caribbean (Virgin Islands, Guadeloupe, Barbados, Netherland Antilles, Colombia), England, Portugal. Mediterranean.

**SPECIMENS STUDIED.**—Carrie Bow Cay: JN-6686 (⊕), epiphytic on *Stylopodium zonale*, 20–23 m depth, fore reef slope, 27 Apr 1977; JN-6805 (♀, ⊕), 18 m depth, outer ridge of fore reef, legit JN and KB, 27 Apr 1977; JN-6842a (⊕), epiphytic on *Dictyota*, 10 m depth, spur and groove zone of inner fore reef, legit JN and KB, 29 Apr 1977.

**REMARKS.**—The publication date of Dillwyn's *British Confervae*, in which *Conferva denudata* was first validly published, has been the subject of debate. We follow Dixon's (1960:309, 317) interpretation that publication date of the work is probably the late autumn (?) of 1809.

Apparently a physiologically tolerant species, *Polysiphonia denuda* occurs in North American and European temperate waters (Taylor, 1962; Parke and Dixon, 1976), as well as in the American tropics.

### ***Polysiphonia exilis* Harvey**

FIGURE 108

*Polysiphonia exilis* Harvey, 1853:47.—Howe, 1920:570.—Taylor, 1928:183; 1960:581.—Hollenberg, 1968b:200, figs. 1c, 3c.—Oliveira Filho, 1977:151.

**DESCRIPTION.**—Thalli dark brown, with an extensive creeping system; trichoblasts formed in radial sequence in erect and prostrate axes, but erect filaments arising cicatrigenously and more or less unilaterally from adaxial scar cells; branches replacing trichoblasts developmentally; rhizoids cut off from pericentral cells; pericentral cells 8 (–10). Spermatangial branches oblong, 50 × 150 µm, and sometimes subtended by trichoblasts, which arise one per segment.

**TYPE-LOCALITY.**—Key West, Florida.

**DISTRIBUTION.**—Tropical Atlantic (except Car-

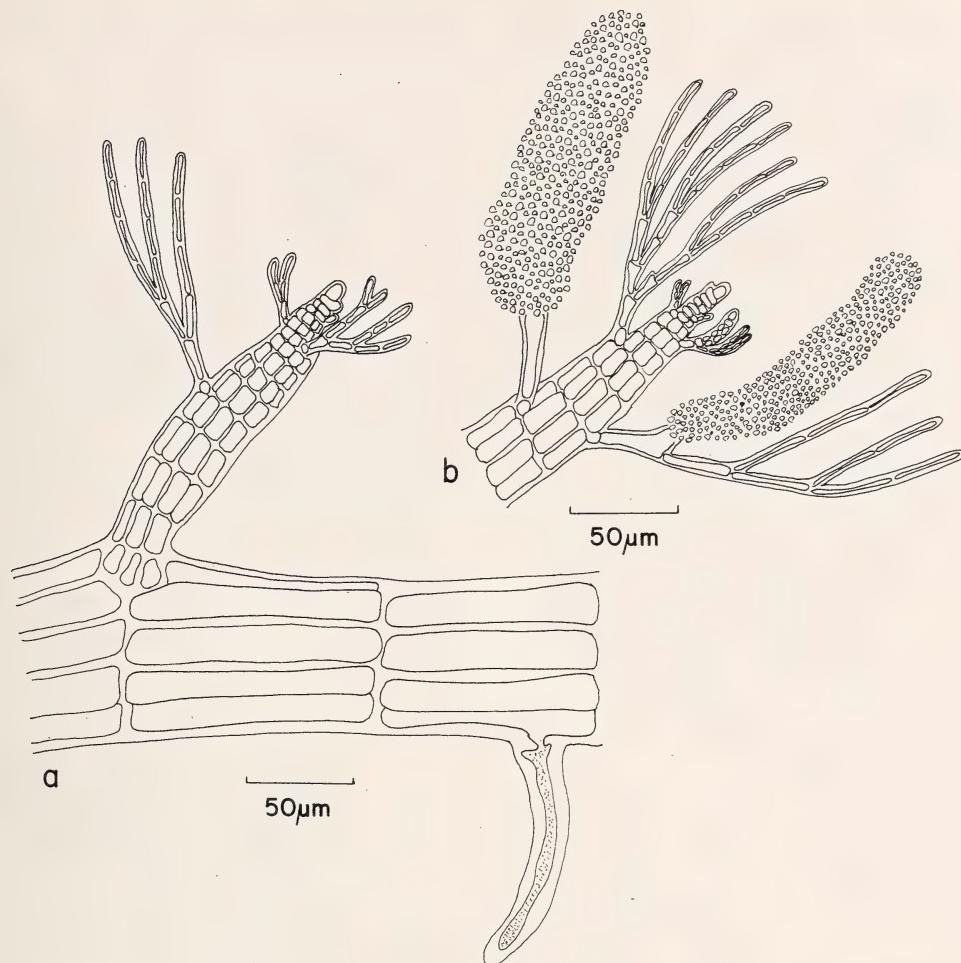


FIGURE 108.—*Polysiphonia exilis*: a, prostrate axis with adventitious branch development, rhizoids cut off from pericentral cells (JN-6342); b, spermatangial branches, note trichoblasts arising one per segment (JN-6342).

ibbean, up to now) and Pacific oceans.

SPECIMENS STUDIED.—Carrie Bow Cay: JN-6342a-c ( $\delta$ ), epiphytic on *Dictyota dichotoma*, ~20 m depth, outer ridge of fore reef, 5 Apr 1976.

REMARKS.—This is the first record of this species in the Caribbean Sea. The Carrie Bow Cay specimens apparently also represent the first spermatangial plants observed in this species (Taylor, 1960; Hollenberg, 1968b).

### ***Polysiphonia ferulacea* Suhr**

FIGURE 109

*Polysiphonia ferulacea* Suhr in J. Agardh, 1863:980.—Collins and Hervey, 1917:124.—Børgesen, 1918:277, figs. 277–

280.—Howe, 1920:570.—Taylor, 1928:183, pl. 24: figs. 16–18, pl. 25: fig. 15, pl. 26: figs. 11, 15; 1960:578.—Oliveira Filho, 1969:128, pl. 24: figs. 141–144; 1977:151.—Taylor and Bernatowicz, 1969:36.—Taylor, 1969:183.—Taylor and Rhyne, 1970:15.—Yoneshigue-Beraga, 1972: 27, pl. 6: figs. 30–31.—Richardson, 1975:130, pl. 23: fig. 7.—Kapraun, 1977:320, figs. 32–37.

DESCRIPTION.—Thalli erect, to 4 cm tall, from a discoidal base; alternately branched from a distinct main axis; older plants with extensive decumbent branches secondarily attached by rhizoids cut off from pericentral cells; branches replacing trichoblasts in development; pericentral cells 4; branches characteristically basally constricted; spermatangial branches cylindrical, 50

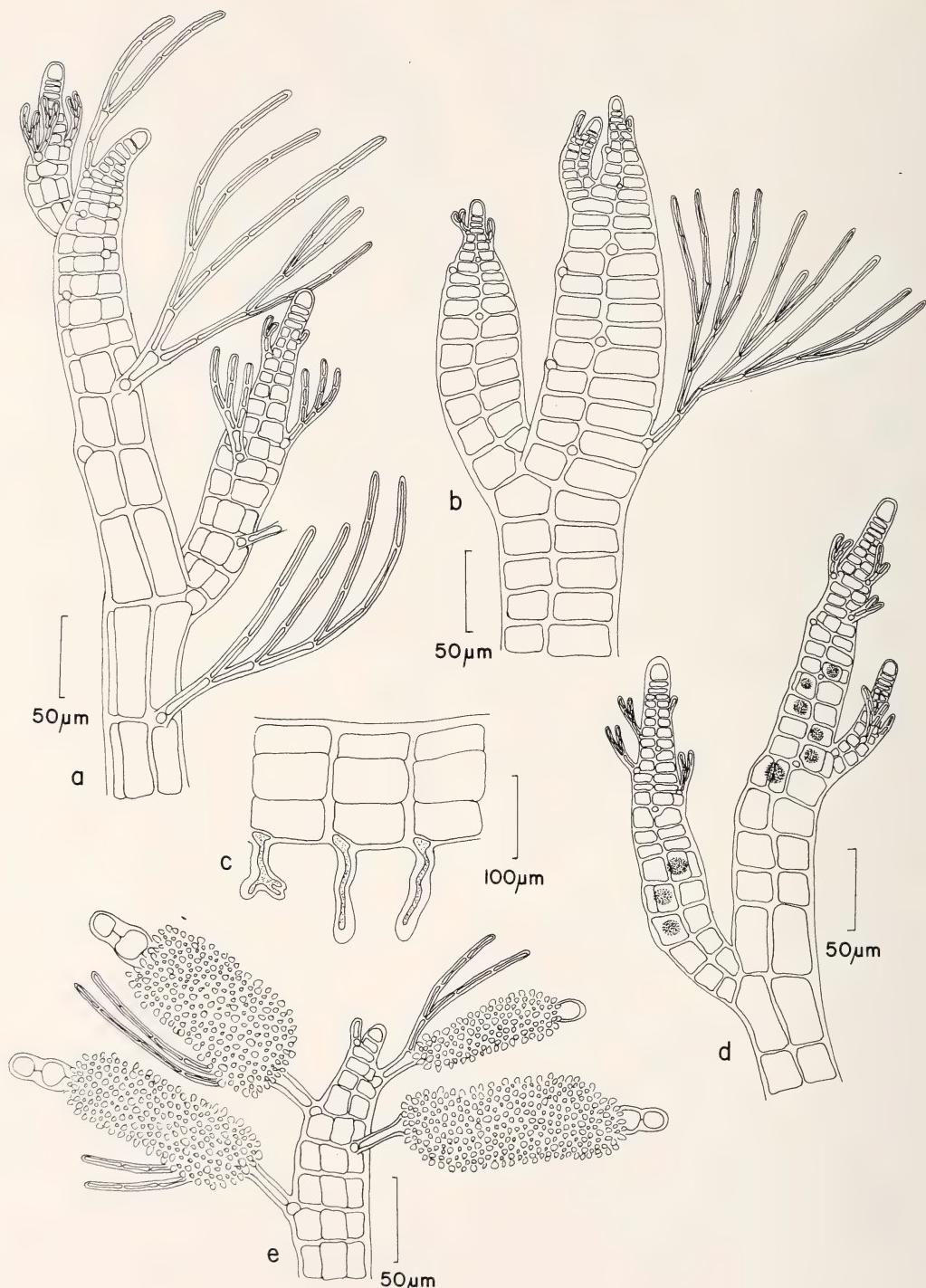


FIGURE 109—*Polysiphonia ferulacea*: a, b, variation in erect filaments on the same plant in respect to cell height-width ratios (DK-s.n., 21 Mar 1978); c, rhizoids cut off from pericentral cells (DK-s.n., 21 Mar 1978); d, tetrasporangia in spiral series (DK-s.n., 21 Mar 1978); e, spermatal-gial branches with characteristic enlarged sterile tip cells (JN-6938).

$\times$  150  $\mu\text{m}$ , with 1–2 conspicuous, thick-walled sterile tip cells. Tetrasporangia in spiral series in branch tips.

TYPE-LOCALITY.—Atlantic Coast of Mexico.

DISTRIBUTION.—Widespread in subtropical and tropical seas; Caribbean: Puerto Rico, Virgin Islands, St. Kitts, Antigua, Guadeloupe, Dominica, Barbados, Trinidad, Venezuela, Curaçao, Costa Rica, Cayman Islands, Jamaica, and Hispaniola.

SPECIMENS STUDIED.—Carrie Bow Cay: JN-6334 ( $\varphi$ ) and JN-6335 ( $\varphi$ ), epiphytic on *Dictyota cervicornis*, 20 m depth, outer ridge of fore reef, 5 Apr 1976; JN-6335 ( $\oplus$ ), epiphytic on *Lobophora variegata*, 25 m depth, fore reef slope, 5 Apr 1976; JN-6410 ( $\oplus$ ), epiphytic on *Valonia ventricosa*, and JN-6413, epiphytic on *Caulpera verticillata*, both from high-relief spur and groove zone (vicinity of IMSWE transect, between 300–400 m markers), 5–6 m depth, legit JN and KB, 27 Apr 1977; JN-6691b, 20 m depth, fore reef slope, 27 Apr 1977; JN-6938 ( $\delta$ ), epiphytic on *Udotea*, 10 m depth, low-relief spur and groove zone of inner fore reef (~10 m S of IMSWE transect line between the 400–500 m markers), legit JN and KB, 23 Apr 1977; JN-6987, 0.5 m depth, entangled with turf of *Jania*, *Centroceras*, and *Wrangelia*, reef crest in front of Carrie Bow Cay Laboratory, legit JN and KB, 22 Apr 1977; DK-s.n. ( $\delta$ ,  $\oplus$ ), eulittoral on cinderblock wall, 21 Mar 1978.

REMARKS.—The close resemblance and hence possible taxonomic confusion between *Polysiphonia ferulacea* Suhr in J. Agardh and *P. sparsa* (Setchell) Hollenberg has been previously noted (Hollenberg, 1968a; Kapraun, 1977). In the present study, specimens of *P. ferulacea* varied greatly in trichoblast development and cell length to width ratios of erect filaments. Although some individuals had short segments as in *P. sparsa*, the presence of characteristic spermatangial branches with sterile tip cells seems to confirm our identification as *P. ferulacea*.

### ***Polysiphonia flaccidissima* Hollenberg**

FIGURE 110

*Polysiphonia flaccidissima* Hollenberg, 1942:783, figs. 8, 19; 1961:351, pl. 2: fig. 2; 1968a:63, figs. 2a, 11.—Brauner,

1975:128, figs. 2–4.—Abbott and Hollenberg, 1976:688, fig. 634.—Hollenberg and Norris, 1977:4, fig. 2E.—Kapraun, 1979:107, figs. 8–9.

DESCRIPTION.—Thalli minute, extensive creeping system giving rise to erect filaments up to 1.5 cm tall; pericentral cells 4; erect and prostrate axes with radial development of branch primordia; branches arising in axils of trichoblasts; rhizoids cut off from the proximal end of pericentral cells. Tetrasporangia to 75  $\mu\text{m}$  in diameter, in spiral series in branch tips; spermatangial branches oblong, 40  $\times$  170  $\mu\text{m}$ , lacking sterile tip cells and subtended by a trichoblast; mature pericarps oval, 150  $\times$  175  $\mu\text{m}$ .

TYPE-LOCALITY.—Laguna Beach, Orange County, California.

DISTRIBUTION.—Atlantic: North Carolina, Gulf of Mexico; Pacific: Southern California, Hawaii, Phoenix and Marshall Islands.

SPECIMENS STUDIED.—Carrie Bow Cay: JN-6351 ( $\delta$ ,  $\varphi$ ) and JN-6353 ( $\oplus$ ), both epiphytic on *Sargassum hystrix*, 16–20 m depth, outer ridge and fore reef slope, 5 Apr 1976; JN-6842b ( $\oplus$ ,  $\varphi$ ,  $\delta$ ), epiphytic on *Dictyota*, 10 m depth, spur and groove zone of inner fore reef, legit JN and KB, 29 Apr 1977. Twin Cays: JN-6886 ( $\varphi$ ,  $\oplus$ ), epiphytic on *Anadyomene stellata*, 1 m depth, among mangroves on E side of eastern half of Twin Cays, 26 Apr 1977.

REMARKS.—*Polysiphonia flaccidissima* is recorded for the first time in the Caribbean Sea. Superficially, it resembles *P. havanensis* sensu Børgesen (1918:266) (see Kapraun, 1977:316), which is widely distributed in the Caribbean; however, *P. flaccidissima* is clearly distinguished from this taxon by its rhizoids, which are cut off from the proximal end of the pericentral cells rather than occurring in open connection with pericentral cells as in *P. havanensis*. Taylor's (1935) specimens identified as *P. havanensis* could possibly belong here; they need to be re-examined to verify its presence in Belize.

Womersley (1979:479) compared descriptions of *Polysiphonia flaccidissima* (Hollenberg, 1942, 1968a; Abbott and Hollenberg, 1976) with southern Australian and Mediterranean specimens identified as *P. sertularioides* (Grateloup) J. Agardh

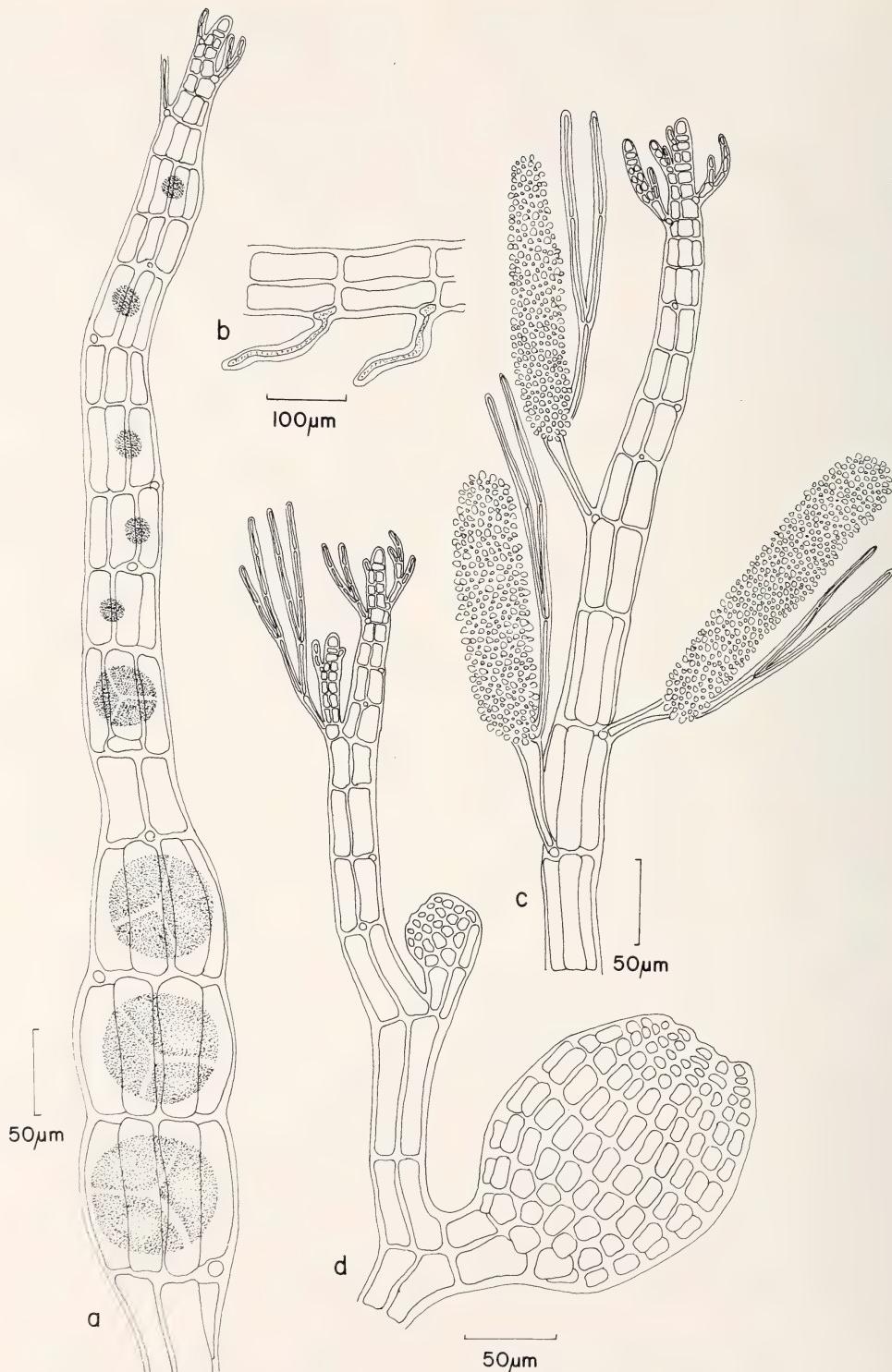


FIGURE 110.—*Polysiphonia flaccidissima*: a, tetrasporangia in spiral series (JN-6351); b, rhizoids cut off from pericentral cells (JN-6351); c, spermatangial branches (JN-6351); d, developing pericarps, note developing vegetative branch in axil of trichoblast (JN-6886).

and concluded that the two species may be synonymous. Until the exact relationship of *P. flaccidissima* to *P. sertularioides* has been determined, we refer material from our present study to *P. flaccidissima*, the name well established in the New World literature (see for instance, Hollenberg, 1942, 1961, 1968a; Hollenberg and Norris, 1977; Brauner, 1975; Kapraun, 1979).

***Polysiphonia scopulorum* var. *villum***  
**(J. Agardh) Hollenberg**

FIGURE 111

*Polysiphonia villum* J. Agardh, 1863:941.

*Lophosiphonia villum* (J. Agardh) Setchell and Gardner 1903: 329.

*Polysiphonia scopulorum* var. *villum* (J. Agardh) Hollenberg, 1968a:81, fig. 7A.—Hollenberg and Norris, 1977:14, fig. 8B., figs. 640–641.

**DESCRIPTION.**—Thalli minute, to 0.5 cm tall, extensive creeping system giving rise to erect filaments; pericentral cells 4; erect filaments arising endogenously in unilateral fashion, at regular intervals of 2–4 segments, from prostrate axes; erect filaments with conspicuous trichoblasts dichotomously branching up to the fourth order; erect branches replacing trichoblasts in development; rhizoids in open connection with pericentral cells. Tetrasporangia in long straight series.

**TYPE LOCALITY.**—“... ad littus [sic] americae tropicae” (J. Agardh, 1863:941); probably the Pacific Coast of Mexico (Hollenberg 1968a:81).

**DISTRIBUTION.**—Widely distributed in northern Pacific and western Atlantic oceans.

**SPECIMENS STUDIED.**—Carrie Bow Cay: JN-6357 (♀), epiphytic on *Lobophora variegata*, 20–25 m depth, fore reef slope, 5 Apr 1976. Twin Cays: DK-s.n. (⊕), eulittoral, epiphytic on mangroves, 24 Mar 1978.

**REMARKS.**—Although this taxon is usually described as having few, slightly branched trichoblasts, our material closely resembles the illustrations in Hollenberg (1968a) showing highly branched, conspicuous trichoblasts in erect filaments. Tsuda and Dawes (1974) list *Polysiphonia scopulorum* in their report on Glover's Reef, Belize, but make no comments on infraspecific relation-

ships. The presence of var. *villum* in the Caribbean is now confirmed.

***Polysiphonia sphaerocarpa* Børgesen**

FIGURE 112

*Polysiphonia sphaerocarpa* Børgesen, 1918:271, figs. 267–271.—

Taylor, 1960:576.—Hollenberg, 1968a:87, figs. 21, 26.—

Taylor, 1969:183.—Taylor and Rhyne, 1970:15.—Kapraun, 1977:318, figs. 26–31, 56.

**DESCRIPTION.**—Thalli small epiphytes, to 1.5 cm tall from a discoidal base; branches dichotomous, becoming decumbent and attached to the substratum by rhizoids cut off from pericentral cells; branches replacing trichoblasts in development; pericentral cells 4. Spermatangial branches cylindrical, 50 × 250 µm, lacking sterile tip cells, with subtending trichoblasts; pericarps spherical, 250 µm diameter, with ostiole of large cells. Tetrasporangia in spiral series.

**TYPE LOCALITY.**—Store Nordsidebugt, St. Thomas, U.S. Virgin Islands.

**DISTRIBUTION.**—Widespread in tropical Atlantic, including the Caribbean (Virgin Islands, Antigua, Dominica, Barbados, Hispaniola), and tropical Pacific oceans.

**SPECIMENS STUDIED.**—Carrie Bow Cay: JN-6746 (♀), JN-6747 (♂), JN-6748 (⊕), and JN-6755 (♀, ⊕), all epiphytic on *Dictyota*, 8 m depth, patch reef, SW of Carrie Bow Cay, legit JN and KB, 25 Apr 1977; JN-6847a (♀), epiphytic on *Sargassum*, 10 m depth, spur and groove zone of inner fore reef, legit JN and KB, 29 Apr 1977; JN-6911 (♀), epiphytic on *Dictyota*, 9–10 m depth, low-relief spur and groove of inner fore reef vicinity of IMSWE transect (Rützler and Macintyre, herein), legit JN and KB, 23 Apr 1977; DK-s.n. (♂, ⊕), eulittoral on reef, 21 Mar 1978.

**REMARKS.**—This species is apparently a member of the “pan-tropical flora” (Kapraun, 1977). Several Carrie Bow Cay specimens have bifurcate spermatangial branches (Figure 112b), which are atypical for this species. Hollenberg (1968a:80, fig. 6f) reported similar variation in male gametophytes of another species of *Polysiphonia*, *P. scopulorum* Harvey from Hawaii.

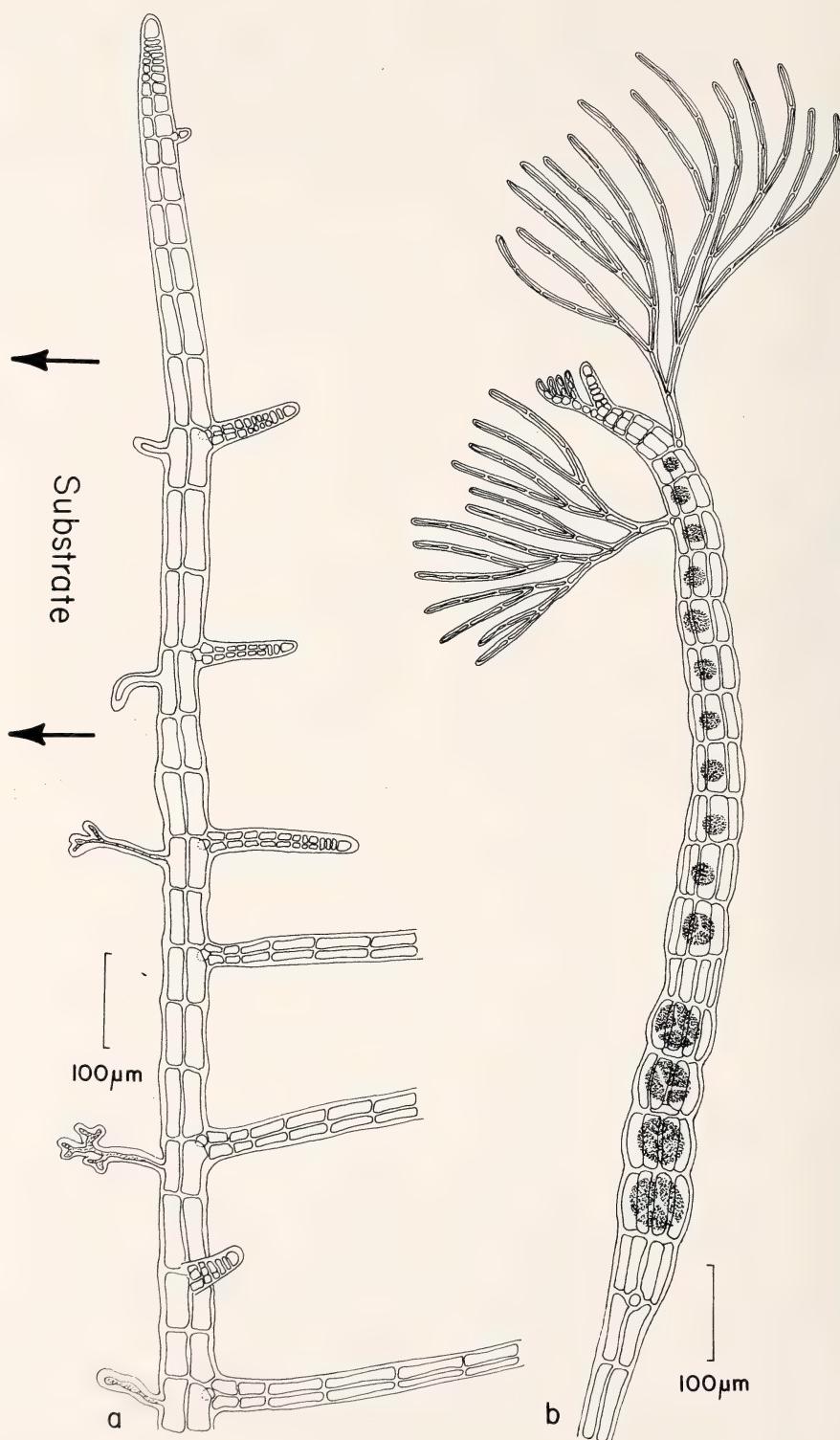


FIGURE 111.—*Polysiphonia scopularum* var. *villum*: a, prostrate axis with rhizoids in open connection with pericentral cells (DK-s.n., 24 Mar 1978); b, erect filament with conspicuous trichoblasts and tetrasporangia in straight series (DK-s.n., 24 Mar 1978).

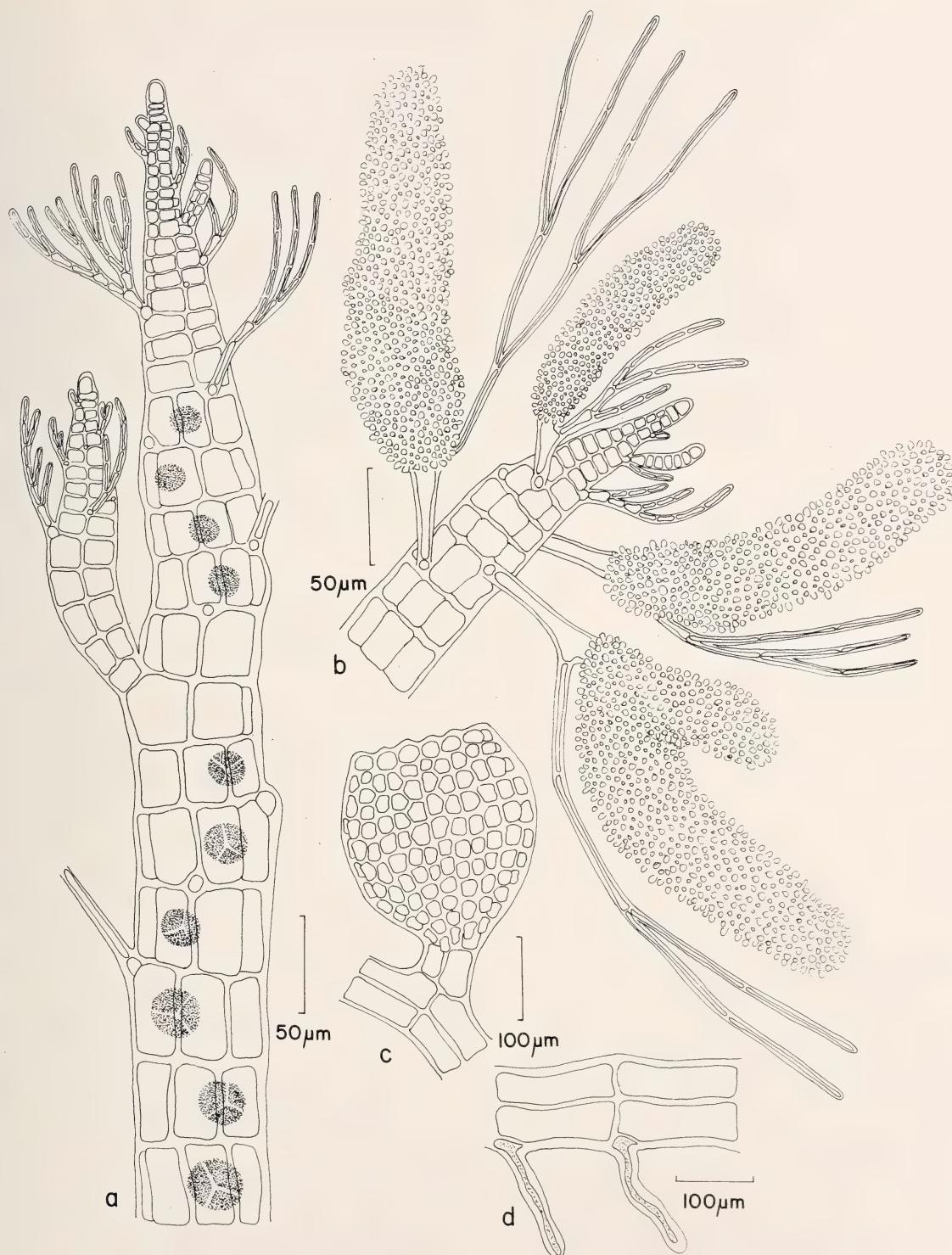


FIGURE 112.—*Polysiphonia sphaerocarpa*: a, tetrasporangia in spiral series (DK-s.n., 21 Mar 1978); b, spermatangial branches (DK-s.n., 21 Mar 1978); c, mature pericarp (JN-6911); d, rhizoids cut off from pericentral cells (DK-s.n., 21 Mar 1978).

## Conclusions

Our collections from Carrie Bow Cay add seven taxa of *Polysiphonia* to the previously reported marine flora of Belize. Five species belong to the subgenus *Oligosiphonia*—*P. atlantica*, *P. ferulacea*, *P. flaccidissima*, *P. scopulorum* var. *villum*, and *P. sphaerocarpa*—and two to the subgenus *Polysiphonia*—*P. denudata* and *P. exilis*. *Polysiphonia exillis* and *P. flaccidissima* are found in the Caribbean Sea for the first time. Prior to this study only *P. havanensis* and *P. scopulorum* were known from Belize, neither of which appeared in our collections. Although we cannot exclude the possibility that *P. scopulorum* reported by Tsuda and Dawes (1974) from Glover's reef, only 25 km east of Carrie Bow Cay, may belong to var. *villum*.

*Polysiphonia atlantica* is a new name proposed for *P. macrocarpa* Harvey, a later homonym for *P.*

*macrocarpa* (C. Agardh) Sprengel. The identity of C. Agardh's *Hutchinsia macrocarpa*, described from the Antilles but never reported since, remains unknown.

Although members of the genus *Polysiphonia* occur predominantly in tropical waters, *P. ferulacea* ranges into the subtropical Atlantic and *P. atlantica* and *P. denudata* extend even into the temperate Atlantic. The latter two species, at least, are remarkable for their physiological tolerance of such a large range of environmental conditions.

All our collections were made close to Carrie Bow Cay, during March and April. We expect that material sampled during other seasons and at different localities along the barrier reef, on the atolls, and along the mainland coast will contain interesting new finds and will help solve taxonomic problems.

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# Hydroidea (Cnidaria: Hydrozoa) from Carrie Bow Cay, Belize

Barry W. Spracklin

## ABSTRACT

Forty-five species of hydroids were found living on the reef and in the lagoon at Carrie Bow Cay. Collections were made each spring (March–June) from 1974 to 1978. Information was gathered on distribution, abundance, substrates, depth ranges, and reproductive maturity. *Halcordyle disticha* (Goldfuss), *Halecium bermudense* Congdon, and *Halopteris carinata* Allman are the dominant hydroids in the outer reef areas and on patch reefs. *Dynamena cornicina* McCrady was common in all areas of the *Thalassia* (turtle grass) beds. *Eleutheria dichotoma* Quatrefages, *Halecium speciosum* Nutting, and *Egmundella grandis* Fraser are recorded from the Caribbean Sea for the first time. *Plumularia* species is probably a growth form of *P. floridana* Nutting, the gonosome of which is undescribed. *Halecium* species is undescribed; corynid species, cormorphid species, and sertulariid species are undescribed and appear to belong to new genera.

## Introduction

This report on the hydroids of the Belizean barrier reef is based on collections made near Carrie Bow Cay during the spring months of each year from 1974 to 1978. Collections and observations were made at nearly all areas during each of the five years. Many of the hydroids have been photographed in situ and almost all have been observed alive, prior to fixation.

No major collection of hydroids has previously been made from the coast of Belize and little

material from this area of the Caribbean Sea was included by Nutting (1900, 1904, 1915), Fraser (1944, 1947), Gemerden-Hoogeveen (1965), or Vervoort (1968). In addition, most of the previous collections were made over a short period of time during a single year and were examined only after preservation. The major exception was Wedler's (1975) ecological study of the hydroids of Santa Marta (Colombia), which covered a 16-month period.

**ACKNOWLEDGMENTS.**—I thank all of my numerous diving partners. S. Earle, P. M. Kier, M. E. Rice, and K. Rützler collected some of the hydroids; sponges were identified by K. Rützler. C. W. Walker read the manuscript and made numerous useful suggestions.

## Methods

During the spring months (March–June) of a 5-year period (1974–1978) 103 collections of hydroids were made by skin diving and SCUBA diving. Conventional transecting techniques could not be applied readily because of the patchy distribution of hydroids in many areas, the cryptic occurrence of many hydroids, and the problem of identifying species with certainty underwater. Since, in most cases, a portion of each colony was collected for identification, the number of observations of each species has been used for abundance estimates. The large number of hydroids (33 species) discovered on dead gorgonians and scleractinean corals does not necessarily indicate a preference for these substrates. Many small hydroids are commonly found on algae, but these are readily overlooked.

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Many of the hydroids were photographed underwater or on the island before fixation, and most of the athecate hydroids were drawn from photographs. The thecate hydroids were drawn from photographs and by camera lucida from fixed specimens. A reference collection is being prepared.

### Annotated Species List

#### Suborder ATHECATA

##### Family CORYMORPHIDAE

Corymorphid species. Figure 113a.

This hydroid is very similar to *Corymorphia symmetrica* Hargitt from the Phillipines; however, solitary polyps grow out of the ends of branches of the gorgonians *Muriceopsis flava* (Lamarck), *Pseudopterogorgia acerosa* (Pallas), *Gorgia flabellum* Linnaeus, and *G. ventalina* Linnaeus rather than on coralline algae. A mature hydranth has 16 to 22 proximal tentacles (usually coiled at the tip), 25 to 30 oral tentacles and seven to nine nematocyst clusters, each bearing one to three lateral gonophores with no evidence of tentacles. Although corymorphid sp. and *C. symmetrica* clearly belong in the family Corymorphidae, these two species could easily be placed in a separate genus since they both have nematocyst clusters, attach to solid substrates, and lack tentacles on the gonophores or medusa buds.

##### Family TUBULARIIDAE

*Ectopleura grandis* Fraser. Figure 113b.

The identification was made from a colony that had only immature medusa buds.

##### Family HALOCORDYLIDAE

*Halocordyle disticha* (Goldfuss). Figure 113c.

##### Family CORYNIDAE

Corynid species. Figure 113d,e.

This hydroid is common in the spur and groove zones on the encrusting sponge *Monanchora barbadensis* Hechtel and in the reef crest it was found on the boring sponge *Cliona caribbea*

Carter. In the outer reef areas it was found on an unidentified sponge, and once on an unidentified alga growing on a dead gorgonian. It has an oral whorl of four tentacles and a second whorl of eight to ten clusters of three tentacles each. The gonophores, which develop between the two whorls, were released in finger bowls immediately after collection with four apical nematocyst clusters, but no tentacles.

#### Family ELEUTHERIIDAE

*Eleutheria dichotoma* Quatrefages. Figure 113f.

First record from the Caribbean Sea. The medusa has been recorded from the Mediterranean Sea, British Isles, Sweden, and France (Brinkmann-Voss, 1970). Only a single polyp with seven capitate tentacles was found on a blade of turtle grass.

#### Family ZANCLEIDAE

*Zanclea costata* Gegenbaur. Figure 113g.

The perisarc at the base of the hydranth was annulated in the material on *Sargassum* and smooth in the material from the reef crest.

#### Family CLAVIDAE

*Corydendrium parasiticum* (Linnaeus). Figure 113h.

Not listed by Vervoort (1968) from the Caribbean, this hydroid was recorded by Wedler (1975) from Colombia.

*Turritopsis nutricula* (McCrady). Figure 113i.

#### Family BOUGAINVILLIIDAE

*Garveia humilis* (Allman). Figure 113j.

#### Family EUENDRIIDAE

*Eudendrium attenuatum* Allman. Figure 113k,l.

*Eudendrium eximum* Allman. Figure 114a.

*Myrionema hargitti* (Congdon). Figure 114b.

#### Suborder THECATA

##### Family CALICELLIDAE

*Egmundella grandis* Fraser. Figure 114c.

First Caribbean Sea record.

##### Family HALECIIDAE

*Halecium bermudense* Congdon. Figure 114d.

*Halecium namum* Alder. Figure 114e.



FIGURE 113.—Athecate hydroids, *Corymorphidae*—*Eudendriidae*: *a*, corymorphid species, some proximal tentacles removed to show the nematocyst clusters,  $\times 10$ ; *b*, *Ectopleura grandis*, some proximal tentacles removed to show the medusa buds,  $\times 40$ ; *c*, *Halocordyle disticha*,  $\times 12$ ; *d*, corynid species,  $\times 45$ ; *e*, corynid species, oral view,  $\times 60$ ; *f*, *Eleutheria dichotoma*, contracted after fixation,  $\times 60$ ; *g*, *Zanclea costata*,  $\times 30$ ; *h*, *Corydendrium parasiticum*,  $\times 10$ ; *i*, *Turritopsis nutricula*,  $\times 10$ ; *j*, *Garveia humilis*,  $\times 50$ ; *k*, *Eudendrium attenuatum*, main stem and side branch,  $\times 8$ ; *l*, *Eudendrium attenuatum*, male,  $\times 32$ .

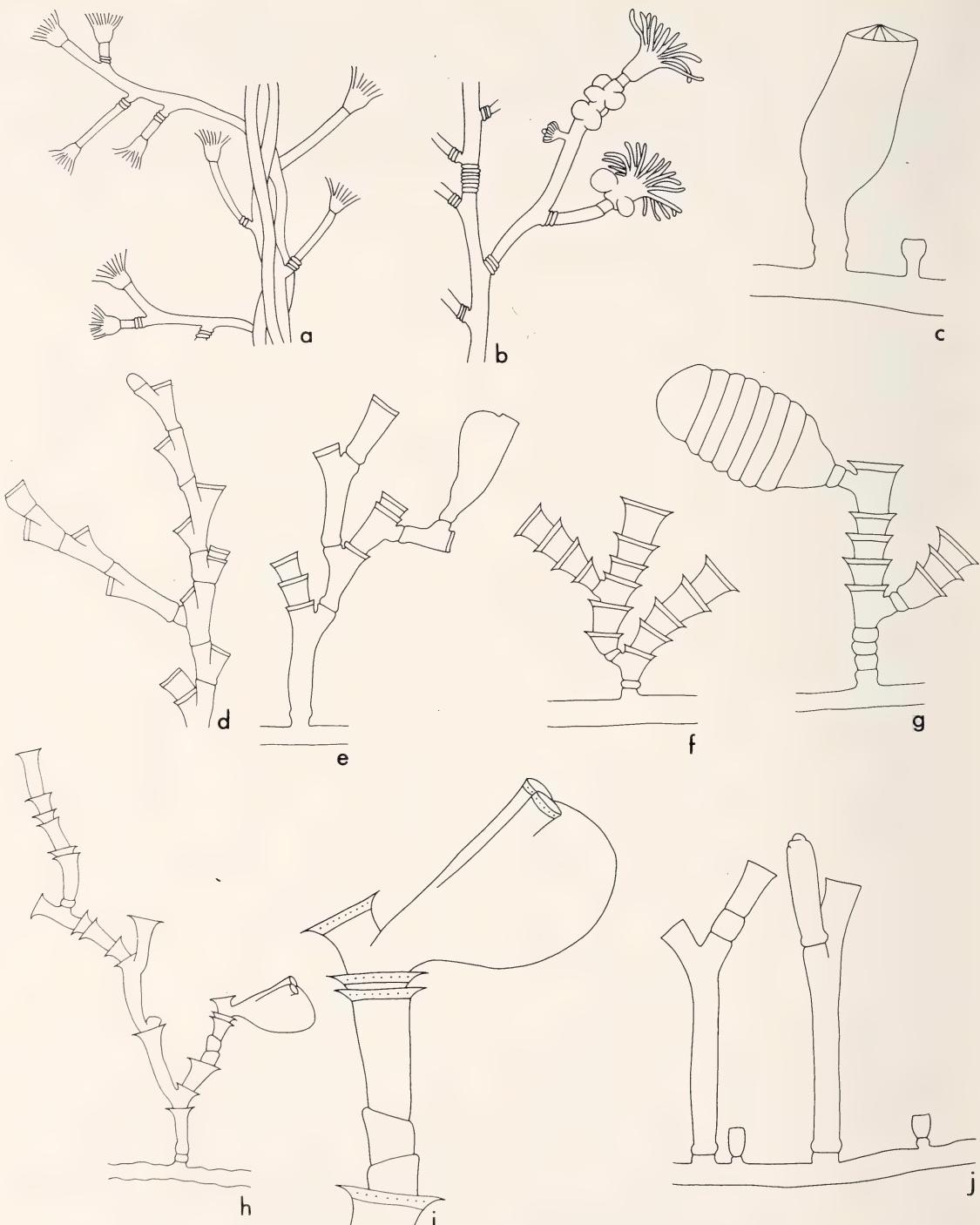


FIGURE 114.—Athecate hydrooids, Eudendriidae (a,b), and thecate hydrooids, Calicellidae—Haleciidae: (c-j) a, *Eudendrium eximium*,  $\times 10$ ; b, *Myriomena hargitti*, main stem and branch of female colony,  $\times 13$ ; c, *Egmundella grandis*,  $\times 130$ ; d, *Halecium bermudense*,  $\times 30$ ; e, *Halecium namum*,  $\times 40$ ; f, *Halecium speciosum*,  $\times 50$ ; g, *Halecium speciosum*, female gonophore,  $\times 50$ ; h, *Halecium* species,  $\times 30$ ; i, *Halecium* species, female gonophore,  $\times 100$ ; j, *Ophiodissa mirabilis*,  $\times 60$ .



FIGURE 115.—Thecate hydroids, Campanulariidae—Sertulariidae: *a*, *Clytia hemisphaerica*,  $\times 30$ ; *b*, *Clytia laxa*,  $\times 25$ ; *c*, *Clytia noliformis*,  $\times 25$ ; *d*, *Obelia dichotoma*,  $\times 40$ ; *e*, *Hebella calcarata*,  $\times 80$ ; *f*, *Hebella venusta*,  $\times 50$ ; *g*, *Scandia mutabilis*,  $\times 80$ ; *h*, *Cnidoscyphus marginatus*,  $\times 15$ ; *i*, *Diphasia tropica*,  $\times 30$ ; *j*, *Dynamena cornicina*,  $\times 40$ .

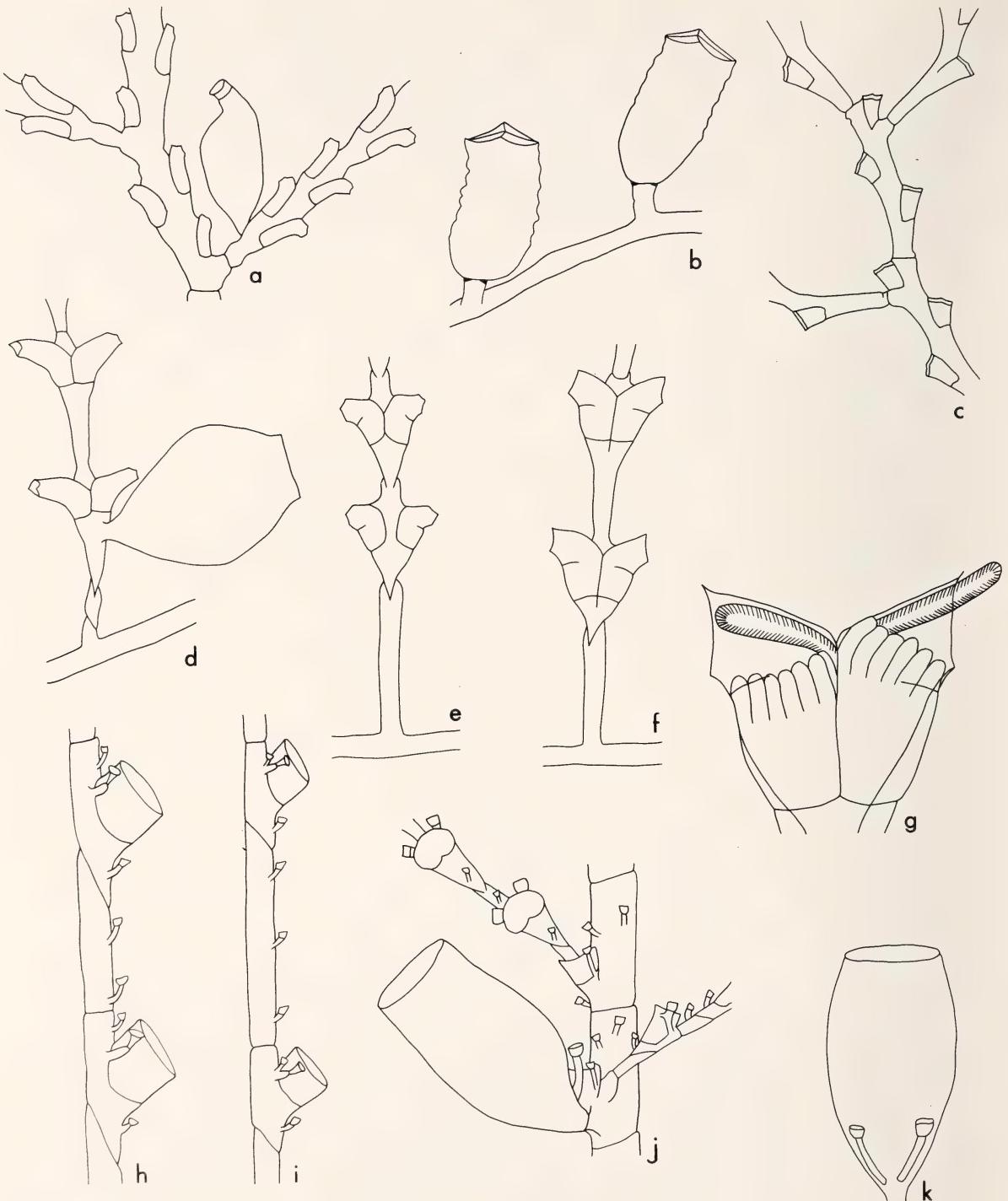


FIGURE 116.—Thecate hydroids, Sertulariidae—Plumulariidae: *a*, *Dynamena crisiodes*,  $\times 20$ ; *b*, *Sertularella parvula*,  $\times 50$ ; *c*, *Sertularella speciosa*,  $\times 15$ ; *d*, *Sertularia stookeyi*,  $\times 25$ ; *e*, *Sertularia turbinata*,  $\times 25$ ; *f*, sertulariid species,  $\times 40$ ; *g*, sertulariid species, showing tentacle-like nematophore,  $\times 130$ ; *h*, *Antenella gracilis*,  $\times 70$ ; *i*, *Antenella quadriaurita*,  $\times 70$ ; *j*, *Halopteris carinata*,  $\times 36$ ; *k*, *Halopteris carinata*, male gonophore,  $\times 36$ .

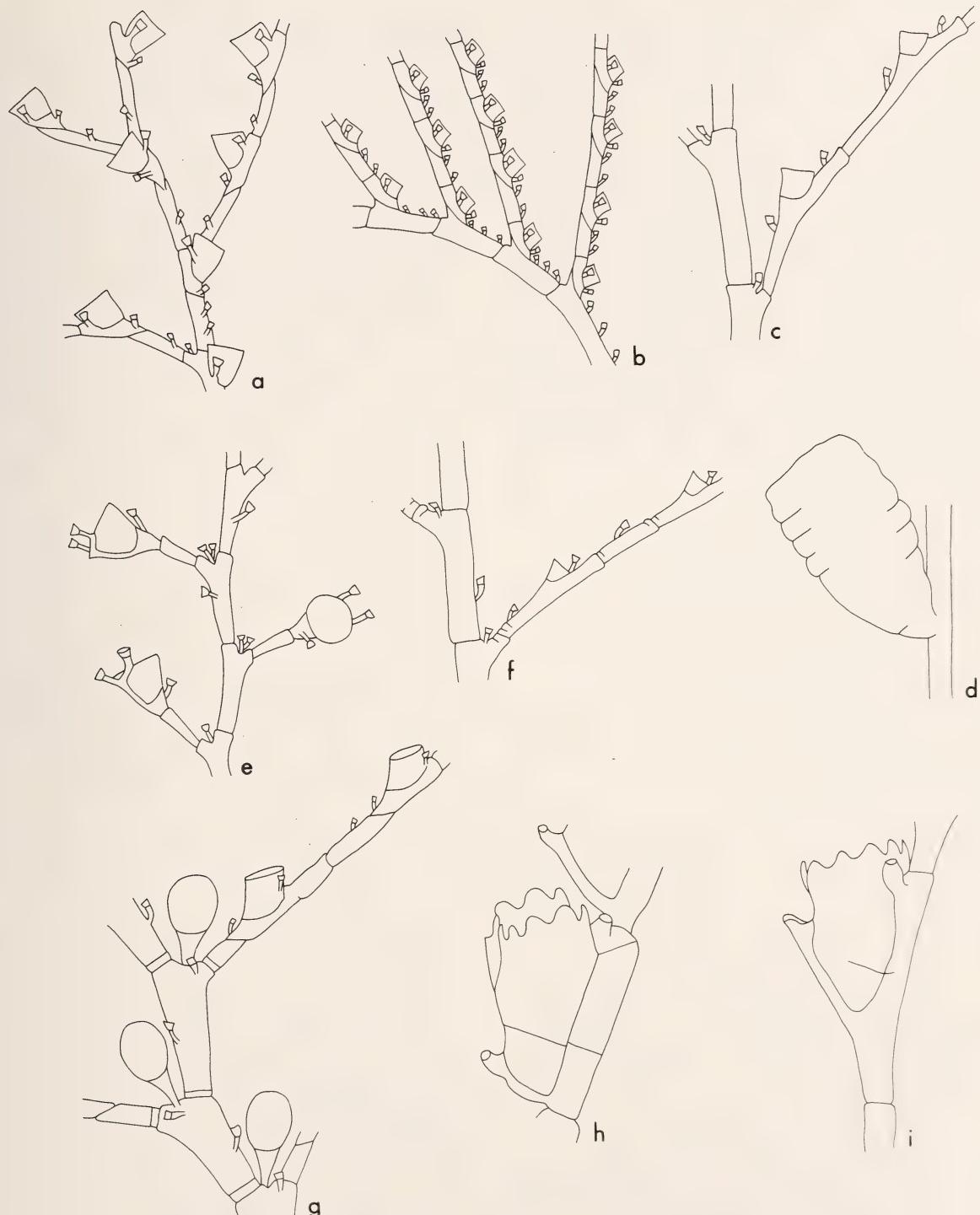


FIGURE 117.—Thecate hydroids, Plumulariidae: *a*, *Halopteris diaphana*,  $\times 35$ ; *b*, *Monostaechas quadridentata*,  $\times 15$ ; *c*, *Plumularia halecioides*,  $\times 35$ ; *d*, *Plumularia halecioides*, gonophore from base of stem or stolon,  $\times 35$ ; *e*, *Plumularia margareta*,  $\times 70$ ; *f*, *Plumularia setacea*,  $\times 60$ ; *g*, *Plumularia* sp.,  $\times 50$ ; *h*, *Aglaophenia latecarinata*,  $\times 130$ ; *i*, *Aglaophenia pluma pluma*,  $\times 130$ .

*Halecium speciosum* Nutting. Figure 114f,g.

Described from the western coast of North America, this is the first record from the Atlantic Ocean.

*Halecium* species. Figure 114h,i.

The colonial growth form and strongly flared hydrophoral margin match the material that Vervoort (1968) referred to *Halecium reflexum* Stechow. Cornelius (1975a) reduced *H. reflexum* to a junior synonym of *H. labrosum* Alder. Vervoort's material was not reproductive and the single gonophore present on my material is similar to *H. nanum* (Figure 114e) and not at all like the gonophore of *H. labrosum*. My material of *H. nanum* from the Carrie Bow Cay area has the normal growth form and hydrophoral margin, and thus *H.* species probably represents an undescribed species.

*Ophiodissa mirabilis* (Hincks). Figure 114j.

Cornelius (1975a) reduced *Ophiodissa caciniformis* (Ritchie) to a junior synonym of *O. mirabilis*.

## Family CAMPANULARIIDAE

*Clytia hemisphaerica* (Linnaeus). Figure 115a.

Listed as *Campanularia* (*Clytia*) *johnstoni* Alder by Vervoort (1968); see Millard (1966) for synonymy.

*Clytia laxa* Fraser. Figure 115b.

Listed as *Laomedea* (*Phialidium*) *laxa* by Vervoort (1968). The genus *Laomedea* was reduced by Cornelius (1975b) to a junior synonym of *Obelia*.

*Clytia noliformis* (McCrady). Figure 115c.*Obelia dichotoma* (Linnaeus). Figure 115d.

Listed by Vervoort (1968) as *Laomedea* (*Obelia*) *congdoni* Hargitt. Cornelius (1975b) referred numerous described species in the genus *Obelia* to three valid species.

## Family LAFOEIDAE

*Hebella calcarata* (A. Agassiz). Figure 115e.*Hebella venusta* (Allman). Figure 115f.*Scandia mutabilis* (Ritchie). Figure 115g.

## Family SERTURLARIIDAE

*Cnidoscyphus marginatus* (Allman). Figure 115h.*Diphasia tropica* Nutting. Figure 115i.*Dynamena cornicina* McCrady. Figure 115j.*Dynamena crisioides* (Lamouroux). Figure 116a.*Sertularella parvula* (Allman). Figure 116b.*Sertularella speciosa* Congdon. Figure 116c.

The distinct hydrothecal base present in all of the shallow water specimens (31 m or less) was totally absent in the colony from 67 m.

*Sertularia stookeyi* Nutting. Figure 116d.*Sertularia turbinata* Lamouroux. Figure 116e.

## Sertulariid species. Figure 116f,g.

Superficially, this hydroid appears to be a normal sertulariid except that, in addition to the hydranth, each hydrotheca contains a large tentacle-like nematophore. In living material, either the nematophore or the hydranth, or both at once, may extend out of the hydrotheca. The operculum is composed of a single plate. This hydroid was collected in 1974 and not seen again until 1978 when it was found to be abundant on the underside of coral rubble in a different area of the reef crest. No reproductive material was evident.

## Family PLUMULARIIDAE

*Antenella gracilis* Allman. Figure 116h.*Antenella quadriaurita* Ritchie. Figure 116i.*Halopteris carinata* Allman. Figure 116j,k.*Halopteris diaphana* (Heller). Figure 117a.*Monostachas quadridentata* (McCrady). Figure 117b.*Plumularia halecioides* (Alder). Figure 117c,d.*Plumularia margareta* (Nutting). Figure 117e.*Plumularia setacea* (Linnaeus). Figure 117f.

## Plumularia species. Figure 117g.

This hydroid is probably conspecific with *P. floridana* Nutting; however, the gonophores were not described and the annulations were somewhat different than in my material. A more reliable identification will have to await an examination of the type material.

*Aglaophenia latecarinata* Allman. Figure 117h.*Aglaophenia pluma pluma* (Linnaeus). Figure 117i.

## Distribution

In order to facilitate collection and recording of data, the lagoon and reef around Carrie Bow Cay were subdivided into 10 areas. The lagoon includes patch reefs, mangrove islands, and the

turtle grass (*Thalassia testudinum* Banks ex König) beds. The reef was divided into the back reef, reef crest, high- and low-relief spur and groove, sand trough, outer ridge, and fore reef slope zones (compare Rützler and Macintyre, herein: 9). The data in Table 18 are the combined results of 103 collections made over a five-year period (1974–1978) and show the distribution, abundance, substrates, reproductive maturity, and depth ranges of the hydroids found in these 10 areas.

**PATCH REEFS.**—The patch reefs have the most diverse hydroid fauna (22 species) in the Carrie Bow Cay area and even adjacent reefs vary considerably in composition and abundance of species. Density of hydroid colonies on the patch reefs is generally greater than that in comparable habitats in the spur and groove, sand trough, and outer ridge zones of the barrier reef. *Halocordyle disticha*, *Halecum bermudense*, *Halopteris carinata*, *Antenella gracilis*, and *Plumularia setacea* are found commonly on dead gorgonians and corals on patch reefs. *Cnidoscyphus marginatus* is unusually abundant at one of the sites, overgrowing large areas of coral rock. A single hydroclad of *Antenella quadriaurita*, the only record of this species in the present collection, occurred on a piece of coral rubble covered with numerous hydrocladia of *A. gracilis*.

**MANGROVE ISLANDS.**—*Dynamena crisioides* is found abundantly and exclusively on the mangrove roots at Twin Cays and Wee Wee Cay. *Myrionema hargitti* and *Halecum bermudense* are concentrated on the mangrove roots and banks at the north end of the channel dividing Twin Cays. *Halecum bermudense*, *Clytia hemisphaerica*, *Obelia dichotoma*, *Dynamena cornicina*, and *Plumularia halecioides* are common on mangrove roots and algae at other locations around the mangrove islands.

**TURTLE GRASS BEDS.**—In view of the large number of turtle grass blades examined and the enormous surface area available for settlement it is surprising that only 12 species of hydroids are found here. *Halecum bermudense* and *Dynamena cornicina* are the only species common throughout and both appear to be most abundant at the eastern sides of Twin Cays and the patch reefs. *Plumularia halecioides*, and to a lesser extent *P.*

*setacea*, are also common on the east side of Twin Cays. The only specimens of *Eleutheria dichotoma* (a single polyp) and *Sertularia stookeyi* (one colony) were collected in this habitat. In many areas of the lagoon, algae replace hydroids as the major epiphytic growth on turtle grass.

**BACK REEF.**—*Dynamena cornicina* and *Plumularia halecioides* are common on the turtle grass in the back reef area between Carrie Bow Cay and the reef crest (0–0.5 m). In 1974 *Myrionema hargitti* was found in a single patch of sand and rubble near the reef crest. Since then, this hydroid has steadily increased in abundance and in 1978 occurred in almost all the sand patches in this area, growing attached to small pieces of rubble in the sand. At the north end of the island, *Halecum speciosum* Nutting was collected on the calcareous green alga *Halimeda* species at a depth of approximately 0.5 m. *Halecum* species and *H. nanum* are also present here on *Halimeda* species; *Halecum bermudense* was collected from the brown alga *Turbinaria* species.

**REEF CREST.**—Most of the nine hydroids from the reef crest were discovered on the underside of coral rubble slightly deeper than the normal low-tide level and were represented, for the most part, by small stolonal colonies. The only common hydroid in this area is "sertularid species." A few hydranths of "corynid species" were collected from one of the reef-crest channels on the boring sponge, *Cliona caribbaea*. *Halocordyle disticha*, *Plumularia inermis*, and *P. setacea* were collected in 2 m of water on dead gorgonians off the end of the reef crest south of Carrie Bow Cay.

**HIGH-RELIEF SPUR AND GROOVE ZONE.**—Only four hydroids were found among the high-relief coral spurs (2–6 m). The most common one in this zone is "corynid species," which occurs under overhanging coral on the sponge *Monanchora barbadensis*. *Halocordyle disticha* and "cormorphid species" were collected on gorgonians at the seaward edge of the high spurs, whereas *Halecum bermudense* was found in crevices among the corals.

**LOW-RELIEF SPUR AND GROOVE ZONE.**—None of the 14 species collected here between depths of 7 and 12 m is abundant, although *Halocordyle disticha*, *Halecum bermudense*, *Halopteris carinata*, and

TABLE 18.—Distribution of Carrie Bow Cay hydroids based on combined data from five collecting seasons, 1974–1978 (representation of abundance estimates; — = absent, 1 = rare, 2 = occasional, 3 = common, 4 = abundant, X = present on a particular substrate, \* = no information; period of reproductive maturity gives earliest and latest dates during observation time that hydroid was collected with gonophores or medusa buds)

Species	Area	Substrate			Period of reproductive maturity	Depth range (m)
			Present	Absent		
Corymorphid species	3	—	—	2	3	3
<i>Ectopleura grandis</i>	—	—	—	—	—	—
<i>Habrocolete disticha</i>	3	—	—	2	3	3
Corynid species	—	—	—	1	—	—
<i>Eleutheria dichotoma</i>	—	—	—	—	—	—
<i>Zanclea costata</i>	—	—	—	—	—	—
<i>Corydendrium parasiticum</i>	2	—	—	—	—	—
<i>Turriopsis nutricula</i>	2	—	—	—	—	—
<i>Gariepa hamilis</i>	—	—	—	—	—	—
<i>Eudendrium attenuatum</i>	2	—	—	—	—	—
<i>E. eximum</i>	—	3	—	4	—	—
<i>Myriomena hargilli</i>	—	—	—	—	—	—
<i>Egmandella grandis</i>	3	3	2	—	2	2
<i>Halecia bermudense</i>	2	—	2	—	—	—
<i>H. nanum</i>	—	—	—	1	—	—
<i>H. speciosum</i>	—	—	—	2	—	—
<i>H. species</i>	—	—	—	—	—	—
<i>Ophiodesma mirabilis</i>	2	3	2	—	2	2
<i>Clytia hemisphaerica</i>	—	—	—	—	—	—
<i>C. laxa</i>	—	—	—	—	—	—
<i>G. noliformis</i>	—	—	—	—	—	—
<i>Sargassum</i>	—	—	—	—	—	—
Algae	—	—	—	—	—	—
Fore-reef slope	—	—	—	—	—	—
Outer ridge	—	—	—	—	—	—
Sand trough	—	—	—	2	2	2
Low spur and groove zone	—	—	—	—	—	—
High spur and groove zone	—	—	—	—	—	—
Reef crest	—	—	2	—	—	—
Back reef	—	—	—	—	—	—
<i>Thalassia</i> beds	—	—	—	—	—	—
Mangrove islands	—	—	—	—	—	—
Reef crests	—	—	—	—	—	—
Back reefs	—	—	—	—	—	—
<i>Thalassia</i> blades	—	—	—	—	—	—
Mangrove roots	—	—	—	—	—	—
Dead corals and sponges	—	—	—	—	—	—
Hydroids	—	—	—	—	—	—
Period of reproductive maturity	26 Apr–20 May	14 May	17 Apr–21 Jun	6 Apr–10 Jun	10 May	15 May
Depth range (m)	4–17	12–27	2–18	0.5–31	0.5	0.2

TABLE 18.—Continued

Species	Area	Substrate	Period of reproductive maturity	Depth range (m)
<i>Obelia dichotoma</i>	Patch reefs			0.2-31
<i>Hebeella calcarea</i>	Mangrove islands	X X	12 Apr	0-31
<i>H. venusta</i>		- -	*	
<i>Sandia mutabilis</i>		- -	*	23
<i>Cnidoscyphus marginatus</i>		- -	*	0.2
<i>Diphasia tropica</i>		- -	*	5-31
<i>Dynamena cornicina</i>	Reef crest	- 1	-	
<i>D. crisioides</i>	Reef spur and groove zone	- 1	-	
<i>Sertularia patula</i>	Reef crest	- 1	-	
<i>S. speciosa</i>	Reef crest	- 1	-	
<i>Serularia strobleyi</i>	Reef spur and groove zone	- 1	-	
<i>S. turbinata</i>	Reef spur and groove zone	- 1	-	
Sertularid species	Reef crest	- 1	-	
<i>Annenella gracilis</i>	Reef crest	- 1	-	
<i>A. quadriaurita</i>	Reef crest	- 1	-	
<i>Halopeltis carnata</i>	Reef crest	- 1	-	
<i>H. diaphana</i>	Reef crest	- 1	-	
<i>Monostacachas quadrifida</i>	Reef crest	- 1	-	
<i>Phumularia halocionides</i>	Reef crest	- 1	-	
<i>P. margareta</i>	Reef crest	- 1	-	
<i>P. selacea</i>	Reef crest	- 1	-	
<i>P. species</i>	Reef crest	- 1	-	
<i>Aglaophenia latecarinata</i>	Reef crest	- 1	-	
<i>A. phuma phuma</i>	Reef crest	- 1	-	
Total number of species	22	10	12	8
Total number of collections	21	9	11	10
		9	10	4
		8	8	9
		7	7	*
		6	6	*
		5	5	*

"cormorphid species" were conspicuous during most dives. The small number of species present in this large area is surprising in view of the greater diversity in deeper water at the adjacent sand trough and in shallower water at the lagoon patch reefs.

SAND TROUGH.—The eight collections made here range from a depth of approximately 13 m at the upper edge of the inner reef slope to about 28 m at the bottom of the trough. This area is called the sand trough, but the 22 species collected here are all from the flanks of the trough, not from the sand fields at the bottom. Although the hydroid fauna is more diverse here than in the spur and groove zones, none of the species is particularly abundant. *Halocordyle disticha*, *Haleciun bermudense*, *Halopteris carinata*, and "cormorphid species" are again the most frequently observed hydroids.

OUTER RIDGE.—Seventeen hydroids were collected mostly on dead gorgonians and corals on the outer ridge at 13–15 m, a depth equivalent to that of the upper level of the sand-trough zone. *Halocordyle disticha*, *Haleciun bermudense*, *Halopteris carinata*, and "cormorphid species" are the most common hydroids.

FORE-REEF SLOPE.—Seven collections were made on the fore-reef slope between 15 and 46 m in depth. *Haleciun bermudense*, *Cnidoscyphus marginatus*, and *Halopteris carinata* are common down to 31 m, whereas *Halocordyle disticha* was collected only occasionally in the upper part of this zone, to a depth of 18 m, and "cormorphid species" was not seen at all. The only hydroid found below 31 m was *Sertularella speciosa*, collected during a bounce dive at 67 m.

SARGASSUM FLOATS.—Hydroids from this substrate, collected whenever the currents carried large amounts of free-floating brown algae of the genus *Sargassum* past the island, are not local in origin. Although present on almost every piece of alga, only seven pieces were recorded from six collections. *Clytia hemisphaerica*, *Obelia dichotoma*, and *Aglaophenia latecarinata* abound in all of the collections. *Aglaophenia latecarinata* is not found on any other substrate.

## Discussion and Conclusions

Forty-five species of hydroids representing 15 families and 29 genera are identified and figured (Figure 113–117). Three species, *Eleutheria dichotoma* Quatrefages, *Haleciun speciosum* Nutting, and *Egmundella grandis* Fraser, have not previously been reported from the Caribbean. A number of unidentified and apparently undescribed species have been collected. *Haleciun* species appears to be undescribed. Three other hydroids, a cormorphid, a corynid, and sertulariid, cannot easily be placed in any known genera and await description (Spracklin, in prep.); in the body of this paper they are referred to as "cormorphid species," "corynid species," and "sertulariid species."

At Carrie Bow Cay, a number of hydroids are sharply restricted in depth of occurrence or substrate preference. For example, *Halocordyle disticha* and "cormorphid species" do not occur below 18 m. *Zanclea costata* is found only on the reef crest and on *Sargassum* at a maximum depth of approximately 0.2 m, *Aglaophenia latecarinata* utilizes only *Sargassum*, and *Dynamena crisioides* grows abundantly and exclusively on mangrove roots. In contrast, *Clytia hemisphaerica* was collected from all six of the substrates examined and *Haleciun bermudense*, the most widely distributed hydroid, was collected from every substrate examined except *Sargassum* and from every area except the reef crest. Only *Haleciun bermudense* commonly utilizes sponges as a substrate.

The depth limitation of *Halocordyle disticha*, to 18 m or less, is particularly interesting since it is reported to 29 m along the eastern United States (Gosner, 1971), but only to approximately 8 m in Colombia (Wedler, 1975). This species is abundant in shallow water and is one of the few hydroids easily recognizable underwater, so that it could not have been overlooked at greater depths. Because this is also the first hydroid to settle on the mooring lines each spring, with colonies appearing usually in three to four weeks, it is very suitable for field studies and manipulation.

The three lagoon areas near Carrie Bow Cay—

the turtle grass beds, mangrove islands, and patch reefs—contain hydroid populations that overlap only slightly. Of the 26 species collected in the lagoon only six (*Halecium bermudense*, *Clytia hemisphaerica*, *Obelia dichotoma*, *Dynamena cornicina*, *Plumularia halecioides*, and *P. setacea*) are found in all three areas. Only *Halecium bermudense*, and *Dynamena cornicina* are common throughout the lagoon.

The back reef, reef crest, and high-relief spur and groove zones have relatively distinct hydroid populations with a different species dominating each zone. In the back reef, *Myrionema hargitti* is the dominant hydroid, whereas “sertularid spe-

cies” is most abundant in the reef crest, and “corynid species” in the high-relief spur and groove zone. In contrast, the outer reef areas appear much more uniform. The same group of four species (*Halocordyle disticha*, *Halecium bermudense*, *Halopteris carinata*, and “cormorphid species”) dominates the low-relief spur and groove, sand trough, and outer ridge zones, with *Halecium bermudense*, *Cnidoscyphus marginatus*, and *Halopteris carinata* also the most abundant hydroids on the fore-reef slope. With the exception of the fore-reef slope, the outer reef zones can be considered as a single area for future hydroid studies.

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# Medusae (Cnidaria) from Carrie Bow Cay, Belize

Ronald J. Larson

## ABSTRACT

Qualitative and quantitative data on medusae from reef, lagoon, and inshore areas near Carrie Bow Cay, Belize are provided. Of 71 species of medusae collected, 57 were found near the reef, 46 in the lagoon, and 21 inshore. Medusae constituted about 10% of the biomass in the samples at the reef and lagoon stations, and 70% inshore. *Liriope tetraphylla* was the most abundant species at reef and lagoon stations. Owing to its abundance and its voracious feeding habits, it is considered to be the ecologically most important species in these two areas.

## Introduction

Coral reefs are known to have an especially diverse plankton "community" (Wood and Johannes, 1975). Recent quantitative studies (Moore and Sander, 1976; Renon, 1977) have examined the dominant groups of mostly lower trophic level species (for instance, copepods), but not the less numerous, although nonetheless important, groups of the higher trophic level such as medusae. Mayer (1900, 1904) and Kramp (1953) have shown that a rich medusaen fauna is associated with coral reefs. These studies, however, lack accurate quantitative data because they were made prior to the development of plankton net flowmeters.

The following study was undertaken to determine the species composition, abundance, and biomass of medusae over a coral reef. Samples taken from a large volume of water over a period

of several months improved the accuracy of biomass and species abundance data. Comparative samples were taken in the near-by lagoon and inshore waters.

**ACKNOWLEDGMENTS.**—I wish to thank J. D. Ferraris, Mount Desert Island Biological Laboratory, for allowing me to examine plankton samples that she collected near Carrie Bow Cay, and K. S. Larson, Smithsonian Institution, for helpful suggestions and for typing the manuscript.

## Study Area and Methods

Sixty-two quantitative plankton samples were taken at three stations (Figure 118) over reefs and in the near-reef lagoon at Carrie Bow Cay, and near the mainland of Belize, between January and April, 1978. A net having  $0.5 \text{ m}^2$  opening,  $560 \mu\text{m}$  mesh diameter, and a flowmeter was used. Surface tows were made between 1730 h and 1830 h for 15–25 min, each filtering an average of  $250 \text{ m}^3$ . Qualitative plankton samples were taken on the reef flat of Carrie Bow Cay. Medusae were also collected by beach seine, by night light and dip net, and while diving. Quantitative samples obtained by J. D. Ferraris during April–May 1976 and May–June 1977 (Ferraris, herein: 143) were also examined.

Whole plankton samples were fixed in 10% formalin. Medusae were sorted later, identified and counted. Wet weights were obtained by gently pouring the preserved plankton, or medusaen sample onto a  $56 \mu\text{m}$  Nitex cloth, blotting it from below and weighing it to the nearest 0.01 g. This method did not damage even very fragile specimens. Dry weights were not measured because the samples are intended for further taxo-

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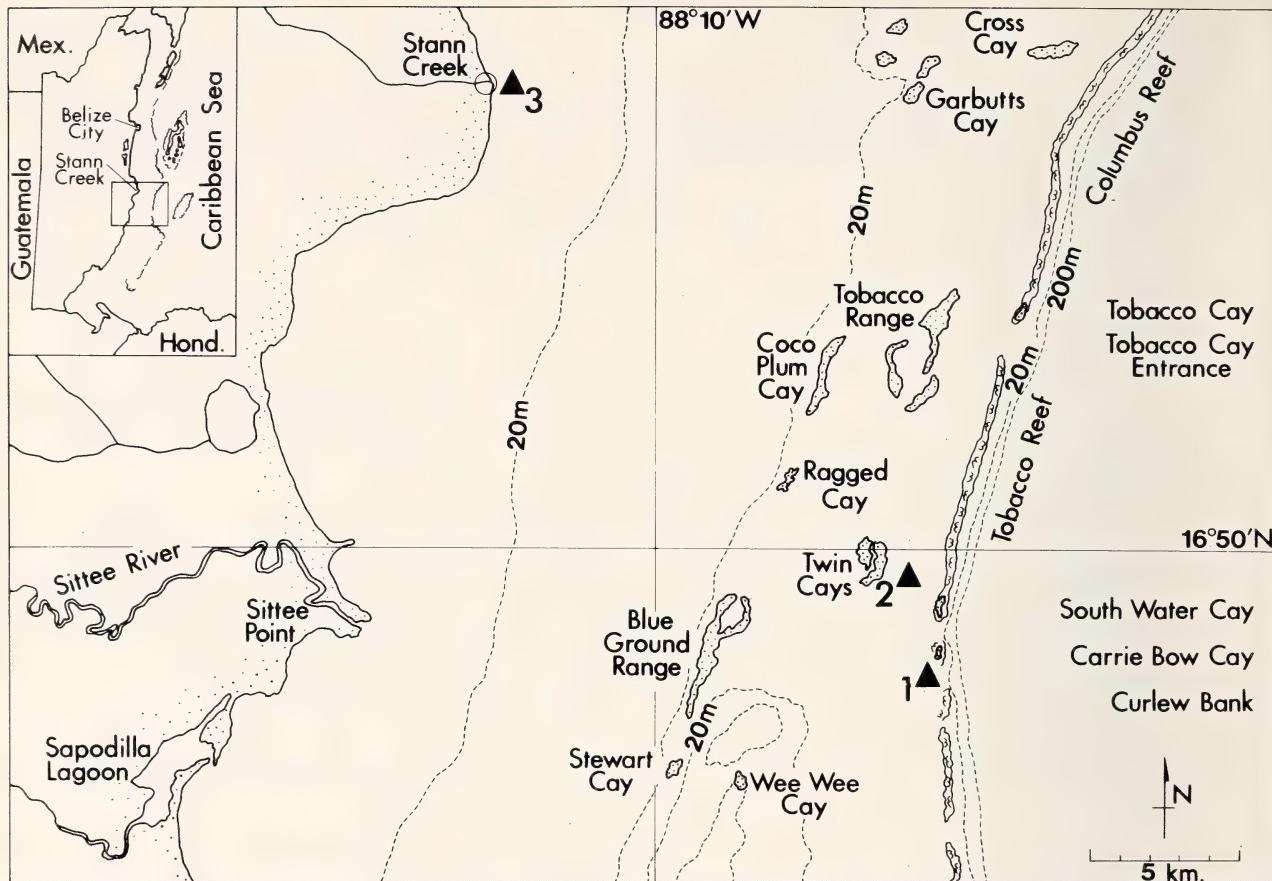


FIGURE 118.—Map of study area near Carrie Bow Cay, indicating collecting stations for medusae (1 = reef; 2 = lagoon; 3 = inshore).

nomic studies.

The stations were located as follows: (1) reef—1 km S of Carrie Bow Cay, about 1.5 km from the shelf edge, 5–8 m depth, patch reefs and sand bottom; (2) lagoon—between South Water Cay

and Twin Cays, about 3 km from the shelf edge, 3–6 m depth, mostly seagrass bottom; (3) inshore—1 km E of the town of Stann Creek (Dangriga), approximately 25 km from the shelf edge, 10 m depth, sand bottom.

### Species List and Distribution

(Letters denote unidentified or new taxa)

	<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>	<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>
Order ANTHOMEDUSAE				<i>Euphyllia</i> species a	+	+
Family CORYNIDAE				<i>Euphyllia</i> species b	+	—
<i>Dipurena halterata</i> (Forbes)	+	+	—	<i>Hybocodon</i> species a	+	—
<i>Sarsia angulata</i> (Mayer)	+	+	—	<i>Propachycordyle</i> species a	+	—
<i>Cladosarsia capitata</i> Bouillon	—	—	+	<i>Vannuccia forbesi</i> (Mayer)	+	—
Family TUBULARIIDAE				Genus A species a	+	—
<i>Euphyllia gracilis</i> (Brooks)	+	+	+	Family HALOCORDYLIDAE		
				<i>Halocordyle disticha</i> (Goldfuss)	+	—

	<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>		<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>
Family CODONIDA incertae sedis				Family EIRENIDAE			
<i>Pachycordyle</i> species a	-	+	-	<i>Eirene lactea</i> (Mayer)	+	-	-
<i>Cnidocodon</i> sp.	+	-	-	<i>Helgicirrha schulzei</i> Hartlaub	-	+	+
Genus B species a	+	-	-	Family AEQUOREIDAE			
Genus C species a	+	-	-	<i>Aequorea macrodactyla</i> (Brandt)	+	+	-
Genus D species a	+	-	-	Order LIMNOMEDUSAE			
Family ZANCLEIDAE				Family OLINDIADIDAE			
<i>Zanclea prolifera</i> Uchida and Sugiura	+	+	-	<i>Cubaia aphrodite</i> Mayer	+	+	+
Family ZANCLEOPSISAE				<i>Olindias tenuis</i> (Fewkes)	+	+	-
<i>Zancleopsis dichotoma</i> (Mayer)	+	+	-	Family PROBOSCIDACTYLIDAE			
Family CLADONEMATIDAE				<i>Proboscidactyla ornata</i> (McCrady)	+	+	+
<i>Cladonema radiatum</i> Dujardin	+	+	-	Order TRACHYMEDUSAE			
Family ELEUTHERIIDAE				Family GERYONIIDAE			
<i>Staurocladia vallentini</i> (Browne)	+	-	-	<i>Liriope tetraphylla</i> (Chamisso and Eysenhardt)	+	+	+
Family CYTAEIDAE				Family RHOPALONEMATIDAE			
<i>Cytæis tetrastyla</i> Eschscholtz	+	+	-	<i>Aglaura hemistoma</i> Pérón and Lesueur	+	+	-
Family HYDRACTINIIDAE				<i>Amphogona apsteini</i> (Vanhöffen)	+	-	-
<i>Podocoryne minuta</i> (Mayer)	+	+	-	<i>Persa incolorata</i> McCrady	-	-	+
<i>Podocoryne ocellata</i> (Agassiz and Mayer)	+	+	-	<i>Rhopalonema velatum</i> Gegenbaur	-	-	+
<i>Podocoryne</i> species a	+	+	+	Order NARCOMEDUSAE			
<i>Podocoryne</i> species b	+	-	-	Family AEGINIDAE			
Family BOUGAINVILLIIDAE				<i>Aegina citrea</i> Eschscholtz	+	+	-
<i>Bougainvillia carolinensis</i> (McCrady)	-	+	+	<i>Solmundella bitentaculata</i> (Quoy and Gaimard)	+	+	-
<i>Bougainvillia frondosa</i> Mayer	+	-	-	Family SOLMARISIDAE			
<i>Koellikerina elegans</i> (Mayer)	-	+	-	<i>Pegantha rubiginosa?</i> (Kölliker)	+	-	-
Genus E species a	+	-	-	<i>Pegantha triloba</i> Haeckel	+	+	-
Family PANDEIDAE				<i>Solmaris corona?</i> (Keferstein and Ehlers)	+	+	+
<i>Amphinema rugosum</i> (Mayer)	+	-	-	Family CUNINIDAE			
<i>Amphinema turrida</i> (Mayer)	+	+	-	<i>Cunina globosa?</i> Eschscholtz	+	+	-
<i>Merga violacea</i> (Agassiz and Mayer)	+	+	+	<i>Cunina octonaria</i> McCrady	+	-	+
<i>Stomotoca pterophylla</i> Haeckel	+	-	-	<i>Cunina peregrina</i> Bigelow	+	+	-
Genus F species a	+	+	+	Order CUBOMEDUSAE			
Order LEPTOMEDUSAE				Family CARYBDEIDAE			
Family DIPLEUROSOMATIDAE				<i>Carybdea alata</i> Reynaud	+	+	-
<i>Dipleurosoma collapsum</i> (Mayer)	-	+	-	<i>Carybdea marsupialis</i> (Linnaeus)	-	-	+
Family LAODICEIDAE				<i>Carybdea</i> species a	+	+	-
<i>Laodicea brevigona</i> Allwein	+	+	-	Family CHIROPALMIDAE			
Family MITROCOMIDAE				<i>Chiropsalmus quadrumanus</i> (Müller)	-	-	+
<i>Tiaropsidium roseum</i> (Maas)	+	+	-	Order CORONATAE			
Family CAMPANULARIIDAE				Family LINUCHIDAE			
"Obelia" sp.	+	+	-	<i>Linuche unguiculata</i> (Schwartz)	+	+	-
<i>Phialidium</i> spp.	+	+	+	Family NAUSITHOIDAE			
Family LOVENELLIDAE				<i>Nausithoe punctata</i> Kölliker	+	+	-
<i>Eucheilota paradoxica</i> Mayer	-	+	+				
Family PHIALUCHIDAE							
<i>Phialicum carolinae</i> (Mayer)	+	+	+				

	<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>		<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>
<b>Order SEMAEOSTOMEAE</b>							
<b>Family PELAGIIDAE</b>							
<i>Chrysaora quinquecirrha</i> (Desor)	—	—	+				
<i>Pelagia noctiluca</i> (Forskål)	+	—	—				
<b>Family ULMARIDAE</b>							
<i>Aurelia aurita</i> (Linnaeus)	+	+	+				
				Totals	57	46	21

## Results

Seventy-one species of medusae were collected during this study. Thirteen species are sufficiently abundant to compare their distribution across the Belizean shelf (Table 19). Six species, *Aglaura hemistoma*, *Amphogona apsteini*, *Nausithoe punctata*, *Sarsia angulata*, *Solmundella bitentaculata*, and *Zanclea prolifera* were collected only near the reef and near-by lagoon. *Carybdea alata* juveniles appeared in nearly one-third of the reef and outer lagoon samples. Since these medusae were collected often with oceanic plankton, for example, gelatinous colonial radiolarians and the blue-green alga *Oscillatoria* sp., and because Bigelow (1938) noted that *C. alata* and representatives of the genera *Amphogona*, *Nausithoe*, *Solmundella*, and *Zanclea* are found in oceanic waters, the above seven species

of medusae may prefer the oceanic conditions near the shelf edge.

Species that dominated inshore samples but were rare or missing over the outer shelf were *Bougainvillia carolinensis*, *Helgicirrha schulzei*, and *Phialidium carolinae*. *H. schulzei* apparently is not restricted to inshore waters (Russell, 1953), but the other two species may be. Mayer (1910) reported that *B. carolinensis* and *P. carolinae* were both very abundant in Charleston Harbor, South Carolina. In her study of hydromedusae from the North Carolina coast, Allwein (1967) found *B. carolinensis* to be restricted to inshore waters. Kramp (1953) noted that *P. carolinae* occurred in the lagoon but not outside the Great Barrier Reef. On several occasions the cubomedusae *Carybdea marsupialis* and *Chiropsalmus quadrumanus* were taken by attracting them to a light at night, and

TABLE 19.—Abundance of dominant medusaen species at each Carrie Bow Cay station  
(presence in at least 33% of samples)

<i>Species</i>	<i>Occurrence in samples (%)</i>			<i>Number of specimens/1000 m<sup>3</sup></i> (Mean and range)		
	<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>	<i>Reef</i>	<i>Lagoon</i>	<i>Inshore</i>
<i>Aglaura hemistoma</i>	55	63	0	37 (0-340)	20 (0-164)	0
<i>Amphogona apsteini</i>	39	23	0	7 (0-47)	4 (0-40)	0
<i>Bougainvillia carolinensis</i>	0	10	100	0	1 (0-13)	4500 (1000-8310)
<i>Cubaia aphrodite</i>	34	32	25	4 (0-15)	3 (0-13)	<1 (0-1)
<i>Helgicirrha schulzei</i>	0	10	100	0	3 (0-48)	108 (31-250)
<i>Liriope tetraphylla</i>	100	100	100	583 (24-5490)	390 (13-1290)	662 (611-690)
<i>Nausithoe punctata</i>	39	41	0	8 (0-105)	8 (0-40)	0
<i>Phialidium</i> spp.	82	86	100	190 (0-2132)	368 (0-3874)	750 (100-1530)
<i>Phialidium carolinae</i>	3	23	100	<1 (0-1)	1 (0-1)	337 (103-610)
<i>Proboscidactyla ornata</i>	29	41	50	5 (0-57)	12 (0-124)	1 (0-6)
<i>Sarsia angulata</i>	39	59	0	32 (0-350)	19 (0-124)	0
<i>Solmundella bitentaculata</i>	47	41	0	18 (0-250)	7 (0-60)	0
<i>Zanclea prolifera</i>	42	36	0	8 (0-60)	7 (0-40)	0

by seining along the beach at Stann Creek. They also are inshore species that the author has observed in similar locations at Puerto Rico.

Ubiquitous species are *Cubaia aphrodite*, *Liriope tetraphylla*, *Phialidium* spp., and *Proboscidactyla ornata*; most of these are cosmopolitan warm-water forms. *Cubaia aphrodite*, however, is restricted to the Caribbean and south Florida-Bahama region. Allwein (1967) found *P. ornata* in both offshore and inshore samples and also noted four species of *Phialidium*, of which *P. languidum* had a similar distribution. It is not known what species of *Phialidium* occur in Belize; the various western Atlantic forms are incompletely described and need revisionary work.

*Liriope tetraphylla* is the only species that occurred in every sample and is relatively abundant at all three stations. Workers have made similar observations of this species in other areas of warm water, including the southeastern United States (Allwein, 1967), Australia (Kramp, 1953), and Brazil (Vannucci, 1963). The importance of *L. tetraphylla* as a carnivore is demonstrated by the fact that many specimens of this medusa had their manubria filled with fish ova, chaetognaths, crustaceans, and other zooplankton. In several samples, more than 40% of *L. tetraphylla* specimens contained fish ova. In the laboratory *L. tetraphylla* is highly active, swimming about with trailing tentacles. This species is so transparent that generally only its shadow is visible and it can easily go unnoticed by prey or predators. So little is known about the biology of this medusa that its role in tropical planktonic ecosystems can only be surmised.

Medusae made up a significant amount of the biomass (wet weight) of samples from all stations (Table 20). At times they constituted more than 50% of the reef and lagoon samples. High variation in biomass and numbers of individuals occurred from day to day, apparently owing to considerable water movement near the outer shelf. Inshore samples were dominated by medusae, which formed nearly 75% of the total plankton biomass collected. Owing to the large mesh of the net, 560 µm, the numerous small copepods

TABLE 20.—Biomass (wet weight) and numbers of specimens of medusae in relation to total net plankton at each station expressed in means (ranges in parentheses)

Station	Medusae		
	Total plankton g/1000 m <sup>3</sup>	Specimens/ 1000 m <sup>3</sup>	
Reef (36 samples)	23 (6-43)	2 (<1-17)	925 (38-5771)
Lagoon (22 samples)	14 (2-33)	2 (<1-15)	900 (34-5047)
Inshore (4 samples)	72 (45-95)	52 (35-61)	6329 (3532-9169)

that occur in tropical inshore areas were obviously not captured.

Seasonal variation in biomass is likely, especially inshore where nutrient input and primary production would increase during the wet season. Since this study, however, represents only a time period within the dry season, the variability is not yet known. One species, *Linuche unguiculata*, did indicate seasonal reproduction. In January 1978, multitudes of recently released *L. unguiculata* ephyrae were found on the reef flat at Carrie Bow Cay. In March small numbers of this medusa, about 5 mm in diameter, were collected at reef and lagoon stations. In May vast numbers of mature *L. unguiculata*, about 15 mm, suddenly appeared along the barrier reef at Carrie Bow and South Water cays (K. Rützler, pers. comm. 1978).

## Conclusions

Seventy-one species of medusae belonging to nine orders were collected at three stations across the Belizean shelf. Fifty-seven species were found near the reef, 46 were collected at the lagoon station, and 21 inshore. The most abundant medusae show three distributional patterns. Species occurring only in the reef and outer lagoon are *Aglaura hemistoma*, *Amphogona apsteini*, *Nausithoe punctata*, *Sarsia angulata*, *Solmundella bitentaculata*, *Zanclea prolifera*, and *Carybdea alata*. Species occurring mainly inshore are *Bougainvillia carolinensis*, *Helgincirha schulzei*, and *Phialicum carolinae*. Ubiqu-

uitous species are *Cubaia aphrodite*, *Liriope tetraphylla*, *Phialidium* spp., and *Proboscidactyla ornata*.

Medusae constituted from 10% to 70% or more of the total plankton biomass retained by a 560  $\mu\text{m}$  net at the three stations. At reef and lagoon stations, medusae formed about 10% of the total sample with a mean value of about 2 g/1000 m<sup>3</sup>, whereas inshore they formed 70% of the total plankton or 52 g/1000 m<sup>3</sup>. At reef and lagoon

stations, a mean abundance of about 900 specimens/1000 m<sup>3</sup> occurred versus inshore abundance of about 6000/1000 m<sup>3</sup>.

*Liriope tetraphylla* was the only species present in 100% of the samples; it also was the most abundant species at reef and lagoon stations. This medusa appears to be ecologically important because of its abundance and also because of its voracious feeding habits.

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## Plates

PLATE 1.—Carrie Bow Cay in relation to the barrier reef of Belize (see also Figure 222): *top left*, discontinuous barrier reef off Ambergris Cay looking SSW; *top right*, barrier reef with cut east of Colson point, Columbus Reef and Southern Long Cay in background; *center left*, continuous shallow reef development north of South Water Cay; *center right*, Carrie Bow and South Water cays on the barrier reef, Twin Cays in the lagoon; *bottom left*, Carrie Bow Cay looking north, June 1972; *bottom right*, Carrie Bow Cay with partly exposed reef flat; yellow laboratory building left of center.

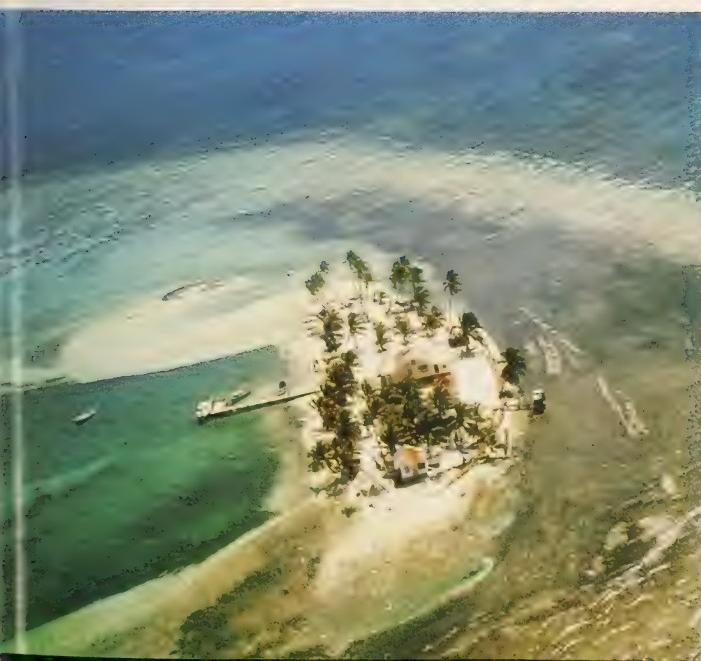


PLATE 2.—Lagoon and back-reef habitats, 0–2 m depth: *top left*, seagrass community, *Thalassia testudinum* and *Dictyota* sp.; *top right*, reef flat seaward of Carrie Bow Cay, *Thalassia testudinum* and *Porites porites* on rubble bottom; *center left*, *Acropora cervicornis* on rubble substrate in patch reef zone, April 1980; *center right*, rubble storm ridge east of Carrie Bow Cay prograding over *Porites astreoides* established on back-reef pavement, March 1975; *bottom left*, inner edge of reef crest with *Porites astreoides*, rubble and pavement zone in background; *bottom right*, community at inner edge of reef crest, with *Halimeda opuntia*, *Porites astreoides*, and *Agaricia agaricites* (Scale = 40 cm).

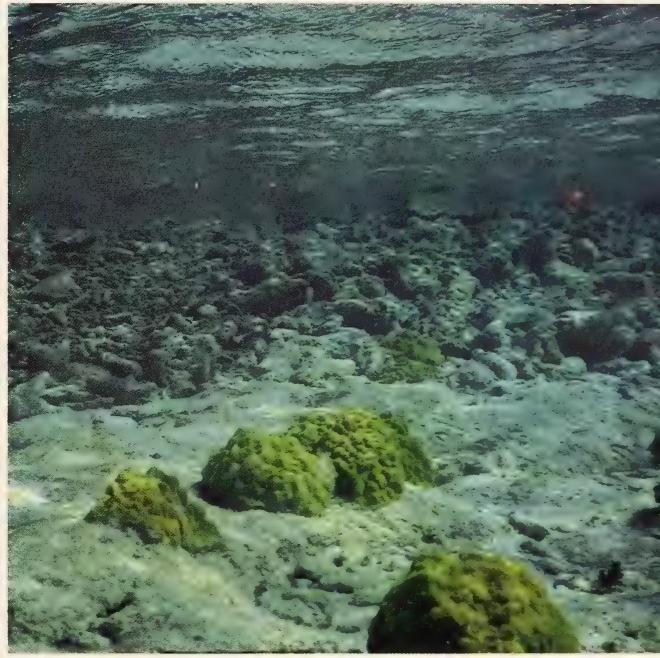


PLATE 3.—Reef crest and high-relief spur and groove zone; *top left*, *Millepora complanata* community, central reef crest; *top right*, *Acropora palmata* thicket, outer edge of reef crest; *center left*, coral pinnacles in transition zone between reef crest and high-relief spur and groove zone, with *Acropora palmata*, *A. prolifera*, *Agaricia tenuifolia*, and *Millepora complanata*, 2 m; *center right*, high-relief spur and groove development, with massive coral heads and octocorals dominating the sand groove, 6 m; *bottom left*, coral buttress formed by association of *Agaricia tenuifolia*, *Porites porites*, and *Millepora complanata*, 3 m; *bottom right*, overhanging flank of coral buttress with prominent *Gorgonia ventalina* and *Pseudopterogorgia* sp., 8 m.



PLATE 4.—Low-relief spur and groove zone and outer fore reef: *top left*, low coral spur covered by coral heads, rubble, and octocorals, sand groove in background, 10 m; *top right*, octocoral community at seaward edge of low-relief spur and groove zone including *Pseudopterogorgia* spp., *Gorgonia ventalina*, and *Eunicea* sp., 14 m; *center left*, top of inner reef slope, columnar growth of *Montastrea annularis* in *Acropora cervicornis* thicket, 17 m; *center right*, *Acropora cervicornis* community on top of outer ridge with corals *Agaricia tenuifolia*, *Montastrea annularis*, *Madracis* sp., and sponge *Agelas* sp., 14 m; *bottom left*, fore-reef slope community, with platy *Montastrea annularis*, a variety of sponges, including *Aplysina fistularis*, *Mycale* sp., *Plakortis* sp., and octocoral *Iciligorgia schrammi*, 30 m; *bottom right*, fore-reef slope community consisting of the corals *Montastrea annularis*, *Madracis decactis*, *Porites porites*, the crinoid *Nemaster rubiginosa*, the octocorals *Plexaura flexuosa*, *Eunicea* sp., *Gorgonia ventalina*, and sponge *Ectyoplasia ferox*.

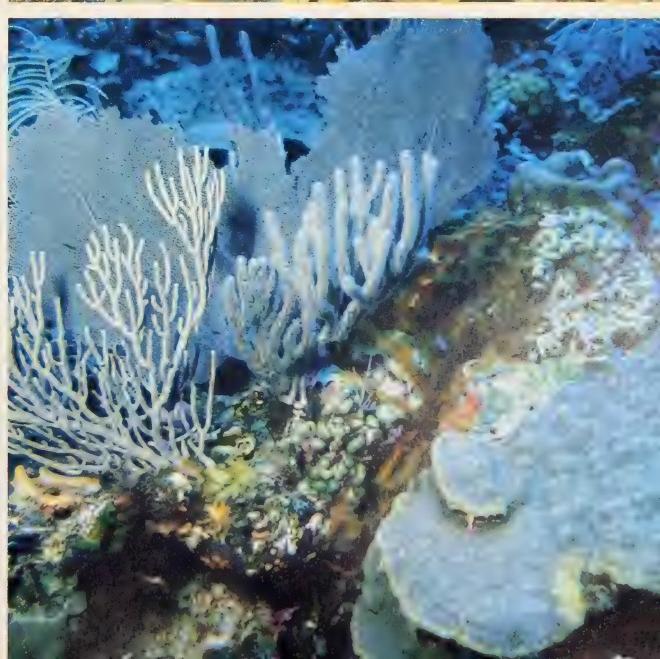
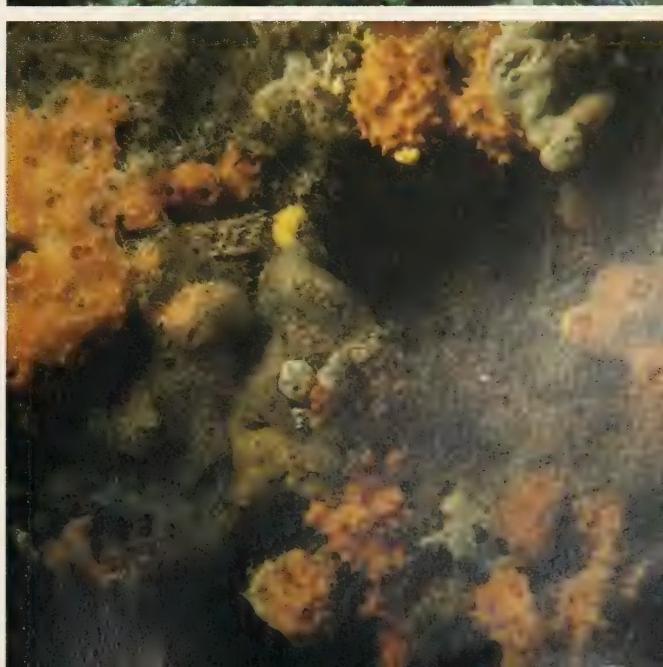
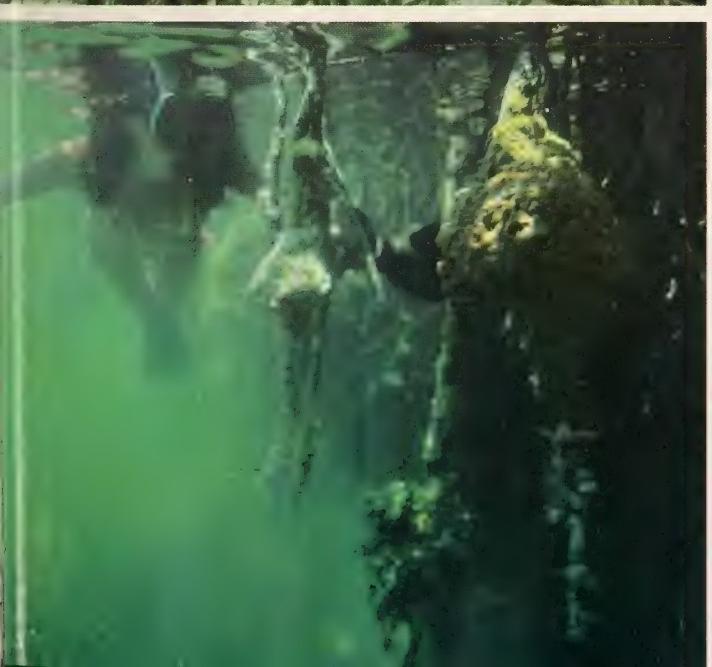
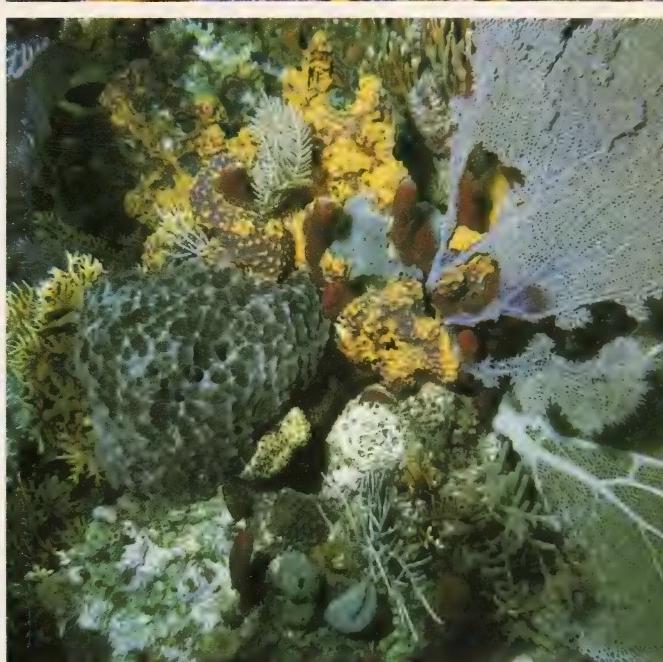


PLATE 5.—Storm ridge and lagoon habitats: *top left*, intertidal rubble field on the reef crest looking northwest; *top right*, representative ophiuroid assemblage under coralline coated coral slab from rubble field consisting of (clockwise from center top) *Ophioderma anitae*, *O. rubicundum*, *O. appressum*, *O. guttatum*, *O. guttatum* lower side, and *O. phoenium*; *center left*, transition zone between lagoon seagrass flat and patch reef, with seagrass *Thalassia testudinum*, corals *Siderastrea siderea* and *Montastrea annularis*, hydrocoral *Millepora alcicornis*, and sponges *Ircinia strobilina* and *Desmapsamma anchorata*; *center right*, patch reef community on dead coral base, with sponges *Ircinia strobilina*, *Pseudoceratina crassa*, *Amphimedon complanata*, and *Niphates digitalis*, hydrocoral *Millepora alcicornis*, and octocoral *Gorgonia ventalina*; *bottom left*, Twin Cays mangrove channel, with *Thallasia testudinum* covered mud bottom and *Rhizophora mangle* roots colonized by fire sponge *Tedania ignis* and sulphur sponge *Lissodendoryx isodictyalis*; *bottom right*, overhanging mud bank in Twin Cay mangrove channel covered predominately by orange sponge *Ulosa ruetzleri* and by unidentified colonial ascidian.





# Stony Corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize

Stephen D. Cairns

## ABSTRACT

Three species of hydrozoan and 42 species of scleractinian corals were identified among 248 specimens collected from maximum depths of 31 m during a survey along the outer edge of the Belizean barrier platform near Carrie Bow Cay and Curlew Bank. This report includes important synonyms, morphological observations, and distributional data, as well as photographs of all species. Diversity of the Carrie Bow Cay coral fauna is high, as compared with adjacent areas of the Caribbean, although not all habitats have yet been equally well searched.

## Introduction

One of the earliest reports on the Scleractinia off Belize (Boone, 1928) recorded two species of deep-water ahermatypes from off Glover's Reef at a depth of 885 m. More recently, Thorpe and Bregazzi (1960) listed 30 hermatypic species from Rendezvous Cay, two of which are considered to be only forms in this account. Stoddart (1962:19) listed 22 reef corals from three atolls off Belize, and York (1971) discussed and figured 24 hermatypes found off the southern shelf of Belize. These numbers have been revised to be consistent with the systematic concept of this paper. Specific references to the coral fauna and reef zonation of Carrie Bow Cay are found in Stoddart (1963:25-26) and in Rützler and Macintyre (herein: 9).

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## Materials and Methods

Most of the corals were collected in March 1978 during a survey of reefs at Carrie Bow Cay and nearby Curlew Bank to a depth of 31 m. All 248 specimens are deposited in the United States National Museum collection (National Museum of Natural History, Smithsonian Institution). Illustrated specimens were collected at Carrie Bow Cay unless otherwise indicated. In some cases, specimens were dyed and then coated with a fine layer of NH<sub>4</sub>Cl in order to improve contrast for photography; these specimens are noted in the figure legends.

Because of inconsistencies in the literature, authors and references are given for all species. Synonymies are restricted to publications in which the species are correctly identified and usefully illustrated. Data on bathymetric ranges apply to the entire geographic range of the species and are taken largely from Goreau and Wells (1967).

## Species List

(\* = ahermatypic)

Class HYDROZOA

Order MILLEPORINA

Family MILLEPORIDAE

*Millepora alcicornis* Linnaeus

*M. complanata* Lamarck

- Order STYLASTERINA  
 Family STYLASTERIDAE  
 \**Styaster roseus* (Pallas)
- Class ANTHOZOA  
 Order SCLERACTINIA  
 SUBORDER ASTROCOENIINA  
 FAMILY ASTROCOENIIDAE  
*Stephanocenia michelinii* Milne Edwards and Haime
- Family POCILLOPORIDAE  
*Madracis decactis* (Lyman)  
*M. mirabilis* (Duchassaing and Michelotti)  
 \**M. pharensis forma pharensis* (Heller)
- Family ACROPORIDAE  
*Acropora palmata* (Lamarck)  
*A. cervicornis* (Lamarck)  
*A. prolifera* (Lamarck)
- Suborder FUNGIINA  
 Family AGARICIIDAE  
*Agaricia agaricites forma agaricites* (Linnaeus)  
 forma *carinata* Wells  
 forma *purpurea* (Lesueur)  
*A. fragilis forma fragilis* Dana  
*A. tenuifolia* Dana  
*A. lamarckii* Milne Edwards and Haime  
*Leptoseris cucullata* (Ellis and Solander)
- Family SIDERASTREIDAE  
*Siderastrea siderea* (Ellis and Solander)  
*S. radians* (Pallas)
- Family PORITIDAE  
*Porites astreoides* Lamarck  
*P. porites forma porites* (Pallas) [= *P. clavaria* Lamarck]  
 forma *divaricata* Lesueur  
 forma *furcata* Lamarck
- Suborder FAVINA  
 Family FAVIIDAE  
*Favia fragum* (Esper)  
*Diploria clivosa* (Ellis and Solander)  
*D. strigosa* (Dana)  
*D. labyrinthiformis* (Linnaeus)  
*Manicina areolata forma areolata* (Linnaeus)  
 forma *mayori* Wells  
*Colpophyllia natans* (Houttuyn)  
*Cladocora arbuscula* (Lesueur)  
*Montastrea annularis* (Ellis and Solander)  
*M. cavernosa* (Linnaeus)
- Family RHIZANGIIDAE  
 \**Phyllangia americana* Milne Edwards and Haime  
 \**Astrangia solitaria* (Lesueur)  
 \**Colangia immersa* Poutalès
- Family MEANDRINIDAE  
*Meandrina meandrites forma meandrites* (Linnaeus)  
 forma *danae* (Milne Edwards and Haime)  
*Dichocoenia stokesi* Milne Edwards and Haime  
*Dendrogyra cylindrus* Ehrenberg
- Family MUSSIDAE  
*Mussa angulosa* (Pallas)  
*Scolymia lacera* (Pallas)  
*S. cubensis* (Milne Edwards and Haime)  
*Isophyllia sinuosa* (Ellis and Solander)  
*Isophyllia rigida* (Dana)  
*Mycetophyllia lamarckiana* Milne Edwards and Haime  
*M. aliciae* Wells  
*M. danaana* Milne Edwards and Haime  
*M. ferox* Wells
- Suborder CARYOPHYLLIINA  
 Family CARYOPHYLLIIDAE  
*Eusmilia fastigiata forma fastigiata* (Pallas)  
 Family FLABELLIDAE  
 \**Gardineria minor* Wells
- Family MILLEPORIDAE**
- Millepora alcicornis* Linnaeus, 1758**
- FIGURE 119a; PLATE 5: center left, center right
- Millepora alcicornis*.—Vaughan, 1901:318, pls. 35, 37–38.—Boschma, 1948:18–19, 23–28, 79–81, 86–88, 100, fig. 6, pl. 14: fig. 3.—Squires, 1958:259, pl. 43: figs. 1–2.—Almy and Carrión-Torres, 1963:144, pl. 2a.—Olivares and Leonard, 1971:59, pl. 5: figs. c–d.—Roos, 1971:43–44, pl. 2.—Smith, 1971:95–96.—York, 1971:5, pl. 1: figs. 1–4.—Tresslar, 1974:123–124, pl. 17.—Colin, 1978:137 [color figs.], 146 [figs.], 150.
- Encrusting or branching colonies up to 50 cm in width. Branches in bushy arrangement or uniplanar, often anastomosing. Surface covered by pores; each gastropore (0.2 mm in diameter) surrounded by 5–7 smaller dactylopoles (0.1 mm in diameter) in an indistinct cyclosystem. Gastrostyles and dactylostyles absent. Orange-yellow or brown.
- HABITAT.—Commonly found encrusting dead gorgonians in fore reef (4–30 m) and in lagoon patch reefs (3–6 m).
- Millepora complanata* Lamarck, 1816**
- FIGURE 119b–c; PLATE 3: top left
- Millepora complanata*.—Boschma, 1948:20, 34–35, 83–84, 94–95, 103, figs. 2a–b, 11, pl. 7: fig. 2.—Squires, 1958:259, pl. 43: fig. 3.—Almy and Carrión-Torres, 1963:144, pl. 2b.—Roos, 1971:44–45, pl. 3.—York, 1971:5, pl. 1: figs. 5–8.—Colin, 1978:140 [color fig.], 143 [figs.], 150.

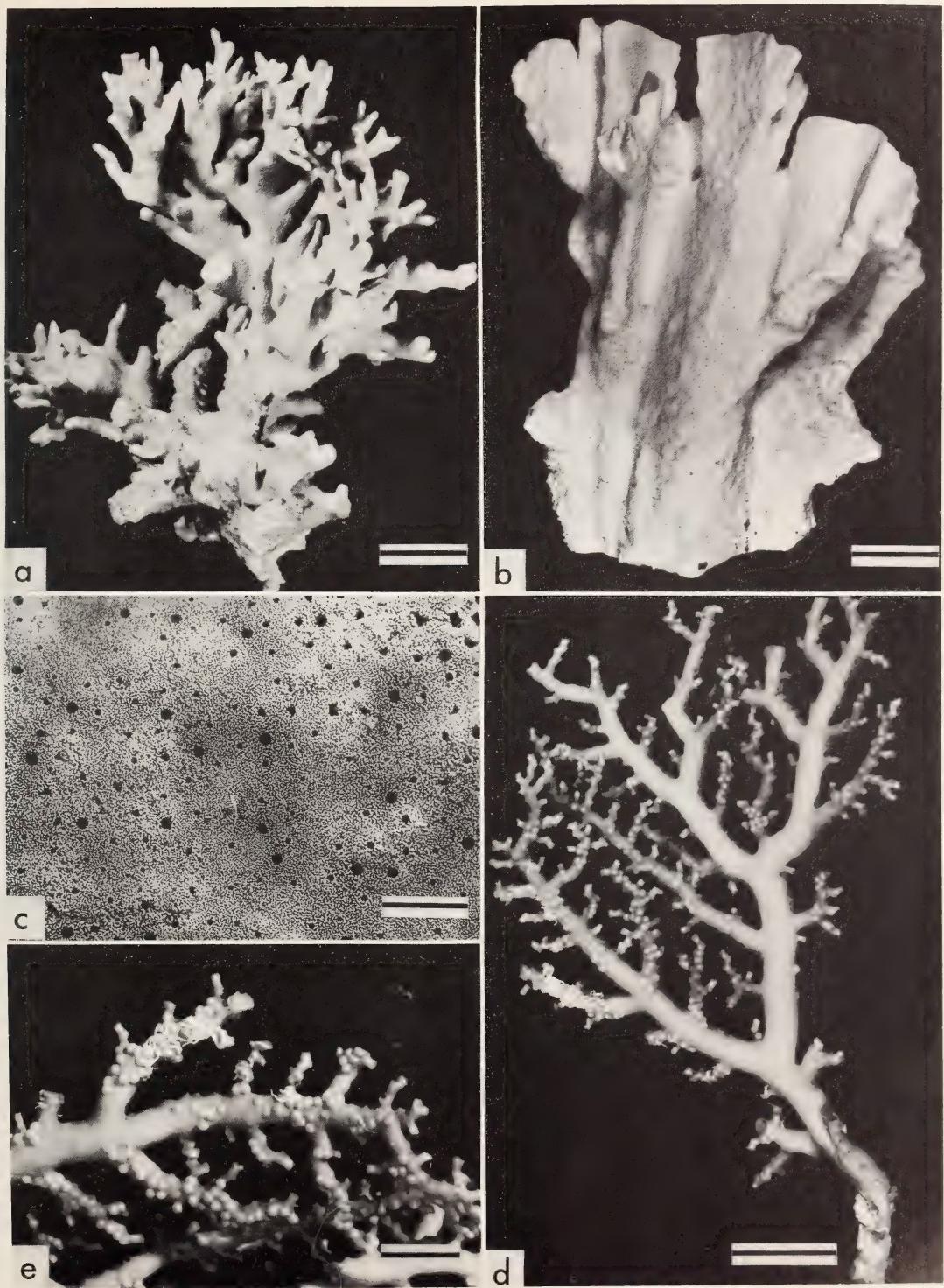


FIGURE 119.—*a*, *Millepora alcicornis*, Bermuda; *b, c*, *M. complanata*, reef crest, 0.5 m, specimen in *c* coated with NH<sub>4</sub> Cl; *d, e*, *Stylaster roseus*, spur and groove zone. (Scale bars: *a, b* = 2 cm; *c* = 0.2 cm; *d* = 1 cm; *e* = 0.5 cm.)

Colony forming thin, smooth, vertical plates united only at their bases. Otherwise, similar to *Millepora alcicornis*.

**HABITAT.**—Major component of reef crest and fore reef spurs (0–8 m).

**DISCUSSION.**—A third western Atlantic species, *Millepora squarrosa* Lamarck, 1816, is characterized by thin, vertical plates with lateral expansions or ridges, which unite with adjacent plates to form a honeycombed complex.

### Family STYASTERIDAE

#### *Styaster roseus* (Pallas, 1766)

FIGURE 119d–e

*Styaster roseus*.—Boschma, 1965:227–247, [4 figs.], pls. 1–3.—Roos, 1971:45, pl. 4: figs. a–b.—Colin, 1978:141 [color fig.], 144 [color fig.], 151.

Small, branching, uniplanar colonies rarely over 10 cm tall. Each gastropore surrounded by 5–15 smaller, slit-like dactylopoles opening on to the gastropore. Gastrostyles and dactylostyles present. Small, hemispherical ampullae commonly present, sometimes in crowded arrangement. Purple, red, or pink.

**HABITAT.**—Very common in spur and groove zone (6–8 m) on undersides of, or within cavities produced by *Agaricia tenuifolia*. Also present on fore-reef slope (20–24 m). Ahermatypic. Bathymetric range: 6–30 m.

### Family ASTROCOENIIDAE

#### *Stephanocoenia michelinii* Milne Edwards and Haime, 1848

FIGURE 120a–b

*Plesiastrea goodei* Verrill, 1900:553–554, pl. 67: fig. 1.

*Stephanocoenia michelinii*.—Squires, 1958:246, pl. 32: figs. 1–2.—Smith, 1971:72, pl. 2.—York, 1971:7, pl. 2: figs. 1–4.—Laborel, 1971:175, pl. 1: fig. 4.—Colin, 1978:209 [color fig.], 211.

*Stephanocoenia intersepta*.—Roos, 1971:51, pl. 4: fig. c, pl. 5: figs. a–b.—Tresslar, 1974:118, pl. 1.

Placoid to cerioid, subhemispherical or encrusting colonies up to 30 cm in diameter. Calices 2–

3 mm in diameter. Twenty-four septa; prominent paliform lobes before first two cycles of septa. Columella large, styliform. Brown.

**HABITAT.**—Only one specimen was collected from the ridge of the outer fore reef (14 m). Bathymetric range: 1–95 m.

**DISCUSSION.**—This species is often mistaken in the field for the more common *Siderastrea siderea* or *S. radians*, which it superficially resembles.

### Family POCILLOPORIDAE

#### *Madracis decactis* (Lyman, 1859)

FIGURE 120c–d; PLATE 4: bottom right

*Madracis decactis*.—Verrill, 1901a:108–109, figs. 2, 2a, pl. 14: fig. 6.—Roos, 1971:52–53, pl. 8: figs. a–b.—Wells, 1973: 19 [key].—Tresslar, 1974:120, pl. 2.—Erhardt and Meinel, 1975, fig. 3.—Colin, 1978:211, 212 [color fig.], 214.

*Madracis decatis*.—Smith, 1971:72–73, pl. 1.

Placoid; nodular, clavate, or thin, encrusting colonies rarely exceeding 15 cm in diameter. Calices about 2 mm in diameter containing 10 septa each. Columella styliform. Noncostate; coenosite bears rows of short spines surrounding each calice. Brown, green, or purplish.

**HABITAT.**—At Carrie Bow Cay found only on outer fore reef (15–24 m). Bathymetric range: 1–70 m.

#### *Madracis mirabilis* (Duchassaing and Michelotti, 1860)

FIGURE 120e–f

*Madracis asperula*.—Roos, 1971:59, pl. 9: fig. b, pl. 10.

*Madracis mirabilis*.—Wells, 1973:19 [key].—Werding and Erhardt, 1976; pl. 4: fig. 1.—Colin, 1978:212 [color fig.], 214, 215 [fig.].

Placoid, ramosa, bushy colonies up to 2 m in diameter. Branches 5–9 mm in diameter with blunt ends. Calices 1–2 mm in diameter; 10 septa each. Columella styliform. Pale cream to bright yellow.

**HABITAT.**—Found in sand trough of outer fore reef (17–22 m) and spur and groove zone (6–8 m). Bathymetric range: 1–60 m.

**DISCUSSION.**—This species has been confused

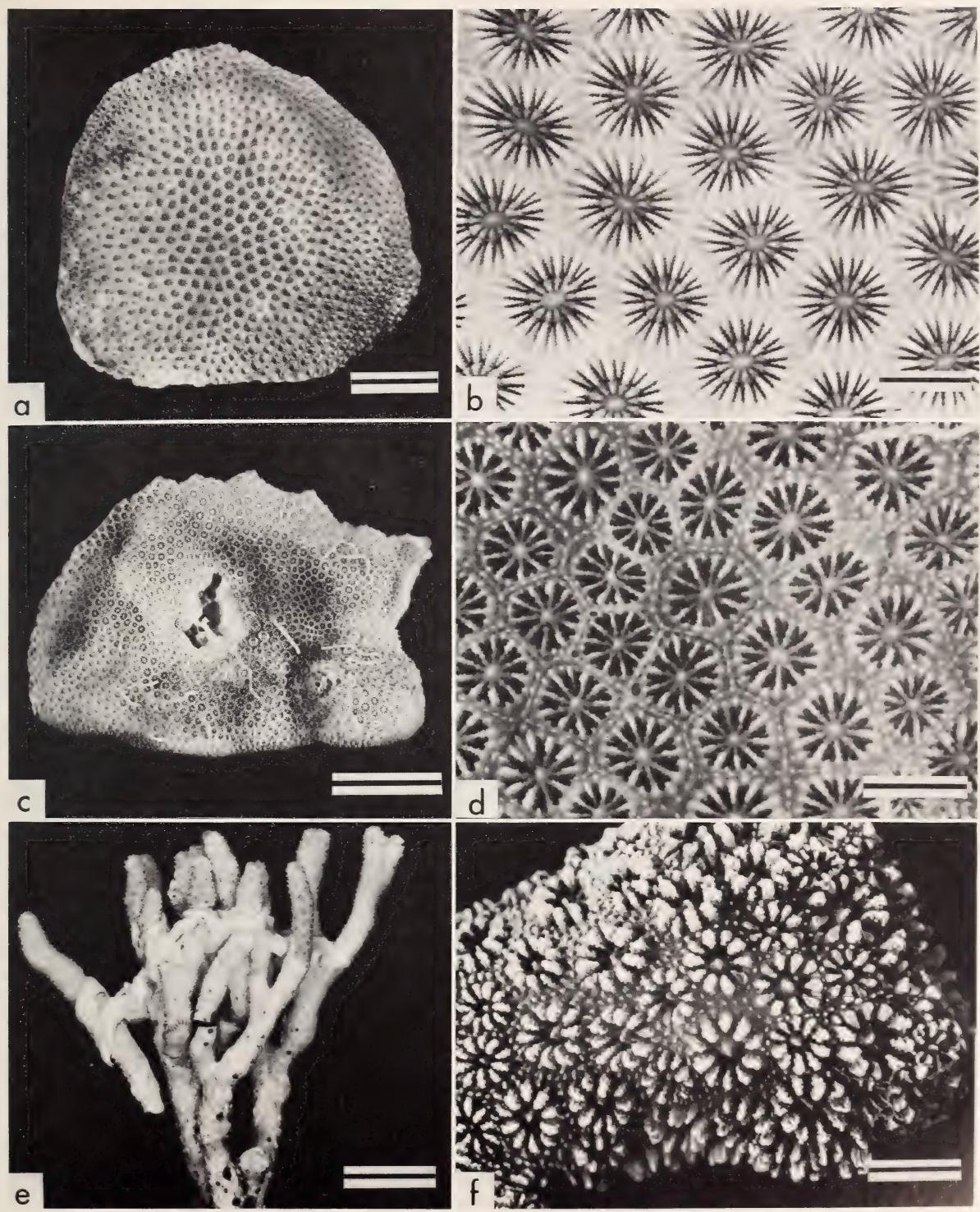


FIGURE 120.—*a, b*, *Stephanocoenia michelinii*, outer ridge, 14 m; *c, d*, *Madracis decactis*, outer ridge, 14 m; *e*, *M. mirabilis*, inner-reef slope, 15–18 m; *f*, *M. mirabilis*, Wee Wee Cay, 1 m, specimen coated with NH<sub>4</sub>Cl. (Scale bars: *a, c, e* = 2 cm; *b, d, f* = 0.2 cm.)

with *Madracis asperula* Milne Edwards and Haime. The latter is distinguished by its more slender branches (2–3 mm) and attenuate branch tips; it is ahermatypic and is usually found in deeper water (to 200 m).

### *Madracis pharensis forma pharensis* (Heller, 1868)

FIGURE 121a

*Madracis pharensis forma pharensis*.—Wells, 1973:18 [key].  
*Madracis pharensis*.—Colin, 1978:213 [color fig.], 214.

Thin, encrusting, stolon-like ribbons or small nodular projections. Calices about 1.5 mm in diameter, each with 20 septa: 10 large, 10 small. Columella styliform. Yellow with pinkish polyps.

**HABITAT.**—All Carrie Bow Cay specimens were found on the fore-reef slope (24–28 m) attached to the undersides of platy *Agaricia* spp. Ahermatypic. Bathymetric range: 20–150 m.

**DISCUSSION.**—*Madracis pharensis forma luciphila* Wells, 1973, forms thick, encrusting, laminar sheets, similar to *M. decactis*. It is hermatypic and has a shallower bathymetric range (2–95 m).

## Family ACROPORIDAE

### *Acropora palmata* (Lamarck, 1816)

FIGURE 121b,c; PLATE 3: top right, center left

*Isopora muricata forma palmata*.—Vaughan, 1901:313–314, pls. 26–27.

*Acropora palmata*.—Squires, 1958:246–247, pl. 34: fig. 1.—Roos, 1971: 55–56, pl. 12: fig. b.—Smith, 1971: 73–74, pl. 4.—York, 1971: 7, pl. 2: figs. 5–8.—Colin, 1978: 36, 216 [color figs.], 218 [fig.], 219, 222.

Broad, flat, frond-like branches, forming colony meters in diameter. Calices 1.0–1.5 mm in diameter, usually on highly exsert, tubular corallites. No axial corallites. Twelve septa. Wall porous. Yellowish brown.

**HABITAT.**—Very common in turbulent shallow waters. At Carrie Bow Cay common directly seaward and shoreward of the reef crest, and at high spur and groove zone (1–8 m); also common

at Curlew Bank (2–4 m). Sparse in back-reef area (1–2 m). Bathymetric range: 0–17 m.

### *Acropora cervicornis* (Lamarck, 1816)

FIGURE 121d; PLATE 2: center left, PLATE 4: center left, center right

*Isopora muricata*.—Vaughan, 1901:312–313, pl. 21, pl. 22: fig. 2.

*Acropora cervicornis*.—Roos, 1971:54–55, pl. 9: fig. a, pl. 12: fig. a.—Smith, 1971:73, pl. 3.—York, 1971:9, pl. 3: figs. 1–2.—Colin, 1978:216, 217 [color figs.], 222–223.

Cylindrical branches, forming colonies up to 3 m in height. Calices about 1 mm in diameter; axial corallites slightly larger. Tubular corallites usually highly exsert. Twelve septa. Wall porous. Yellowish brown.

**HABITAT.**—Common as dense thickets in sand trough and outer ridge of the outer fore reef (24 m); also present in spur and groove zone, back-reef area (1–2 m), and adjacent patch reefs. Bathymetric range: 0–50 m.

### *Acropora prolifera* (Lamarck, 1816)

FIGURES 121e, 122a; PLATE 3: center left

*Isopora muricata forma prolifera*.—Vaughan, 1901:313, pl. 22: fig. 1, pls. 23–25.

*Acropora prolifera*.—Roos, 1971:55, pl. 11.—Smith, 1971:74.—York, 1971: 9, pl. 3: figs. 3–4.—Colin, 1978:217 [color fig.], 223, 226.

Very similar to *Acropora cervicornis*, but branches more crowded, often crossing over and fusing, producing flabelliform or reticulate plates. Usually smaller than *A. cervicornis* and not found in dense thickets.

**HABITAT.**—Found on seaward side of reef crest (0.5–2.0 m) in very turbulent waters. Bathymetric range: 0–30 m.

**DISCUSSION.**—All other characters being similar, the three species of *Acropora* are differentiated by growth form: *A. prolifera* is the intermediate, linking the frond-like *A. palmata* and the rameous *A. cervicornis*. Some authors (Gregory, 1895; Vaughan, 1901) have considered them to be three

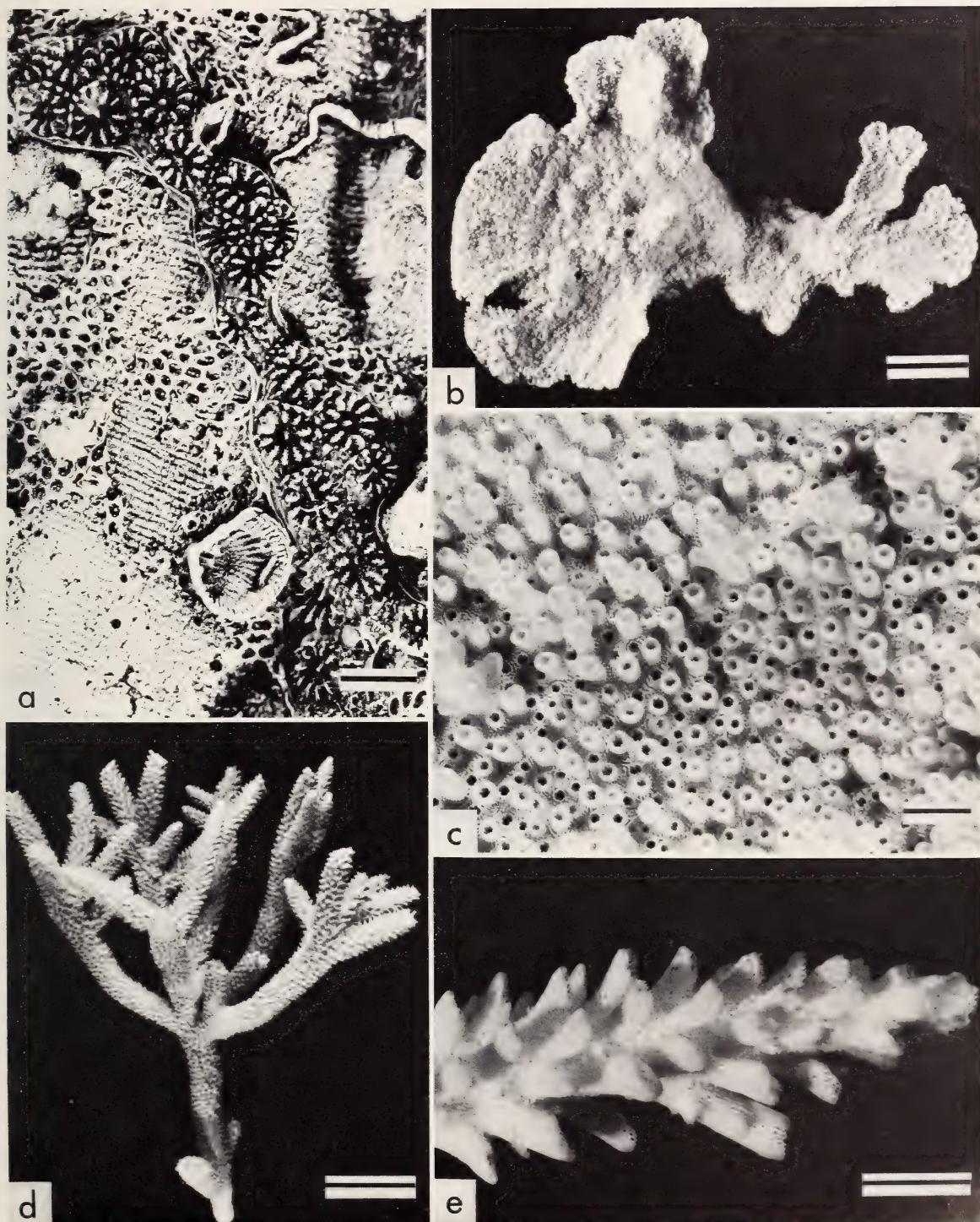


FIGURE 121.—*a*, *Madracis pharensis* f. *pharensis*, fore-reef slope, 24–27 m, on underside of *Agaricia fragilis*, specimen coated with NH<sub>4</sub>Cl; *b*, *c*, *Acropora palmata*, off Cuba; *d*, *A. cervicornis*, exact locality at Carrie Bow Cay unknown; *e*, *A. prolifera*, off Belize, exact locality unknown. (Scale bars: *a* = 0.2 cm; *b*, *d* = 5 cm; *c*, *e* = 0.5 cm.)

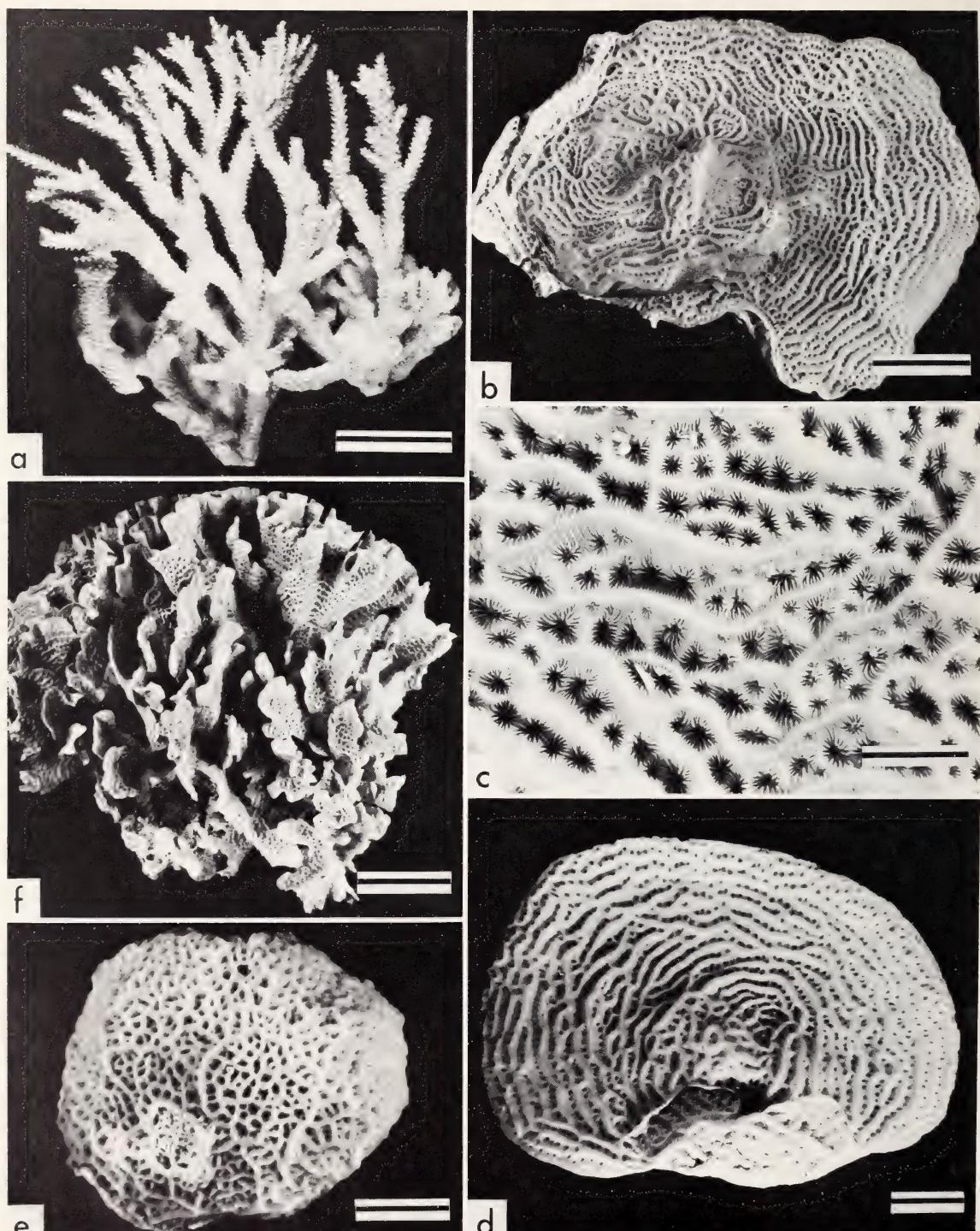


FIGURE 122.—*a*, *Acropora prolifera*, off Belize, exact locality unknown; *b*, *Agaricia agaricites* f. *carinata*, fore-reef slope, 24–27 m; *c*, *d*, *A. agaricites purpurea*, sand trough, 21 m; *e*, *A. agaricites*, patch reef area, 2–3 m; *f*, *A. tenuifolia*, exact locality at Carrie Bow Cay unknown. (Scale bars: *a*, *b*, *f* = 5 cm; *c* = 0.5 cm; *d*, *e* = 2 cm.)

forms of the same species, whereas others (Smith, 1971; Roos, 1971; Wells, 1973) have retained them as separate species. Discussions of the problem can be found in Vaughan (1901:312–314; 1919:482) and in Roos (1971:54).

### Family AGARICIIDAE

#### *Agaricia agaricites* (Linnaeus, 1758)

FIGURE 122b–e

*Agaricia agaricites*.—Verrill, 1901a:146–149 [in part, not variety e], figs. 5–7, pl. 26: figs. 2–3, pl. 27: figs 1–3, 5–7.—Squires, 1958:247–248, pl. 32: fig. 3, pl. 33: figs. 1–3.—Roos, 1971:56–58, pl. 14: figs. a–b.—Smith, 1971:74–75, pls. 5–6.—York, 1971:11, 13 [in part, pl. 4: figs. 3–8, pl. 5: figs. 1–6].—Wells, 1973:25, fig. 6a [not *A. a. fragilis*].—Tresslar, 1974:120, pl. 4.—Colin, 1978:220, 221 [color fig.], 226, 231.

*Agaricia crassa* Verrill, 1901a:145, pl. 30: fig. 6, pl. 34: fig. 2.  
*Agaricia purpurea*.—Verrill, 1901a:149–150, pl. 27: figs. 4a–b.

Colonies massive and encrusting; thick and flat, attached by pedicel; or flat with thick imbricated, vertical, bifacial lobes. Up to 1 m in diameter. Ceriod to meandroid. Calices 1.5–3.0 mm in diameter, arranged in reticulate pattern or in rows of up to 20; 3–7 calices/cm. Columella small. Chocolate to purplish brown.

**HABITAT.**—*Agaricia agaricites* forma *agaricites* is most common in back-reef and patch reef areas (0.5–2.0 m); *A. a.* forma *purpurea* (Lesueur, 1821) is common in the spur and groove zone and outer fore reef (7–30 m); and *A. a.* forma *carinata* Wells, 1973, was collected only from the fore-reef slope (18–30 m). Bathymetric range: 1–70 m.

**DISCUSSION.**—At least five growth forms have been described and named for this variable species and several more forms could be described on the basis of similar criteria. The most common form at Carrie Bow Cay is *purpurea*, a large (up to 1 m), thick, flat colony with 5–6 calices/cm and long valleys having up to 20 calices. Each valley is bordered by prominent collines. Forma *agaricites* is smaller, hemispherical or encrusting, with larger calices arranged in a discontinuous or reticulate pattern and only 3–5 calices/cm. Forma *carinata* is like *purpurea* but has scattered, low (2–3

cm), thick, bifacial crests. The remaining two forms have not been collected at Carrie Bow Cay: forma *humilis* Verrill has small (1.5 mm in diameter), pinched calices in a crowded, reticulate arrangement; and forma *danai* Milne Edwards and Haime is massive with tall, erect, imbricated lobes.

#### *Agaricia fragilis* forma *fragilis* Dana, 1848

FIGURE 123a–b

*Agaricia fragilis*.—Verrill, 1901a: 142–145, pl. 26: fig. 1a–d.—Smith, 1971:75, pl. 8.—Wells, 1973:24 [not fig. 6a].—Colin, 1978:224 [color fig.], 234.

Pedicelled or encrusting, very thin, unifacial fronds, either flat or vase-shaped. Usually less than 15 cm in diameter. Calices about 1.0 mm in diameter, 5–7/cm. Very low or no collines. Chocolate or purplish brown.

**HABITAT.**—Common on fore-reef slope (18–27 m). Bathymetric range: 3–40 m.

**DISCUSSION.**—*Agaricia fragilis* is similar to *A. agaricites* forma *purpurea*, but is distinguished by its thinner, more delicate corallum and its lack of or very small collines. Roos (1971) considered *A. fragilis* a variety of *A. agaricites*.

#### *Agaricia tenuifolia* Dana, 1848

FIGURE 122f; PLATE 3: center left, bottom left

*Agaricia agaricites*.—York, 1971:9, pl. 3: figs. 5–6.

*Agaricia tenuifolia*.—Wells, 1973:25 [key], fig. 13.—Erhardt and Meinel, 1975, fig. 5.—Werding and Erhardt, 1976, pl. 1: fig. 1.—Colin, 1978:224 [color fig.], 227 [fig.], 231.

Large, bushy colonies up to several meters in size, composed of thin, vertical, dissected fronds. Corallum bifacial. Valleys short, sometimes reticulate. Collines prominent. Columella small. Brownish.

**HABITAT.**—At Carrie Bow Cay this species is ubiquitous: it is common in the back-reef area (2–4 m) and is the major component of the buttresses and spurs in the spur and groove zone of the inner and fore reef (5–8 m). It is also found in the sand trough and fore-reef slope (20–27 m). Bathymetric range: 2–27 m.

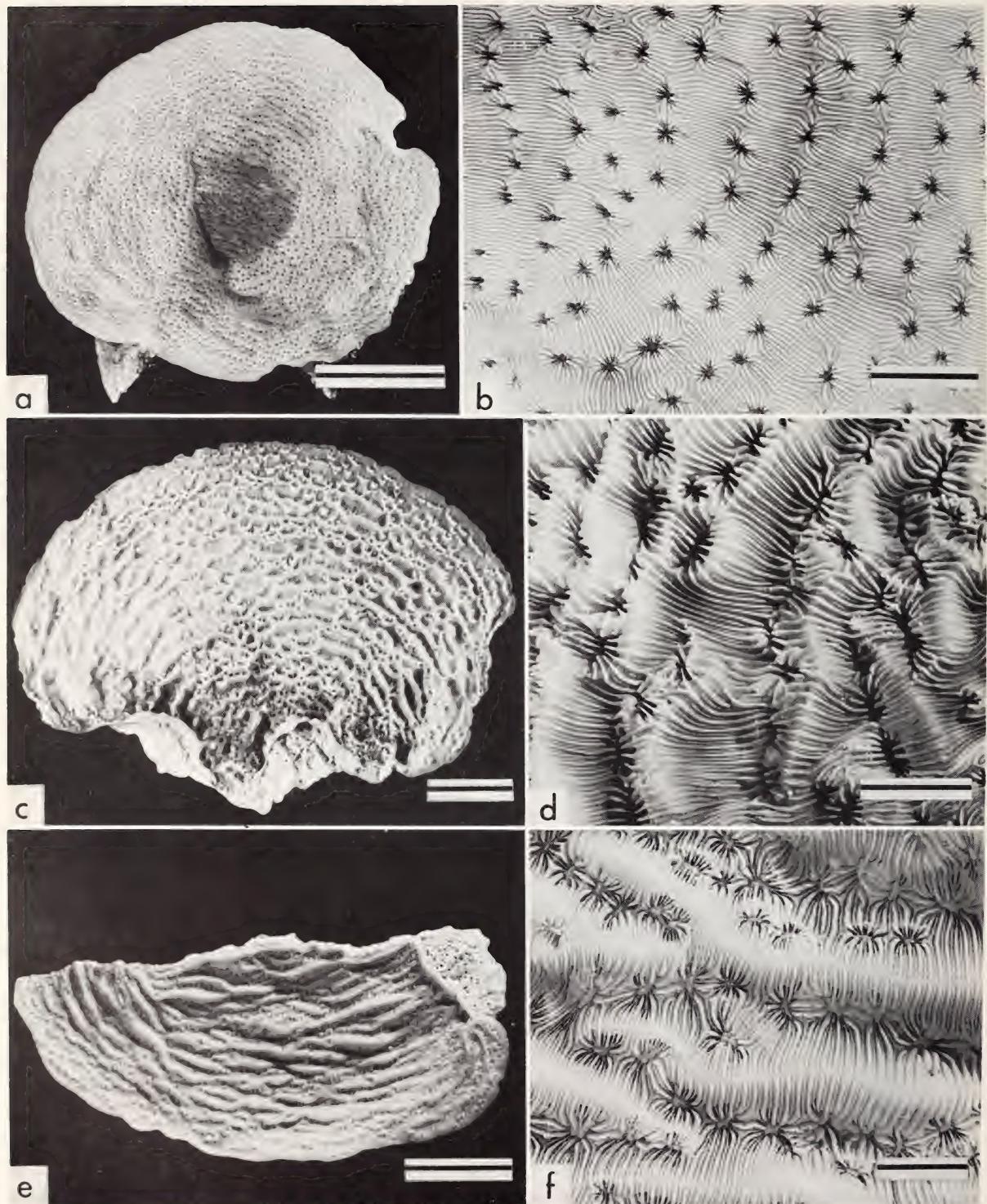


FIGURE 123.—*a, b*, *Agaricia fragilis* f. *fragilis*, fore-reef slope, 24–27 m; *c, d*, *Leptoseris cucullata*, inner reef slope, 15–18 m; *e, f*, *A. lamarckii*, fore-reef slope, 24–27 m. (Scale bars: *a, c* = 5 cm; *b*, *f* = 0.5 cm; *d* = 1 cm; *e* = 2 cm.)

**Agaricia lamarcki Milne Edwards and Haime,  
1851**

FIGURE 123e-f

*Agaricia lamarcki*.—Wells, 1973:26–28, figs. 8–10.—Colin, 1978:234.

Thin, unifacial, centrally attached fronds up to 2 m in diameter. Calices about 2 mm in diameter, 3–5/cm along valley. Valleys long, 4–6 mm wide. Septa thinner than interspaces, alternating in height and thickness. Collines prominent and thick. Columella large.

**HABITAT.**—Collected only on fore-reef slope (25–27 m). Bathymetric range: 4–46 m.

**DISCUSSION.**—Distinguished from *Agaricia grahamae* Wells, 1973, by its thinner septa, which alternate in size, and its wider valleys.

**Leptoseris cucullata (Ellis and Solander, 1786)**

FIGURE 123c-d

*Agaricia nobilis* Verrill, 1901a:150–151, pl. 28: figs. 1–2.—Smith, 1971:75–76, pl. 7.

*Agaricia agaricites*.—Roos, 1971:56–58 pl. 15.

*Helioseris cucullata*.—Wells, 1973:25 [key], figs. 14, 33.—Colin, 1978:229, 232 [color figs.], 234–235.

*Helioceris cucullata*.—Tresslar, 1974:121, pl. 6.

*Leptoseris cucullata*.—Dinesen, 1980:187–188, pl. 1: figs. 1–3.

Very thin, unifacial, pedicelled fronds up to 40 cm in diameter. Underside costate. Calices about 3 mm in diameter, each of which is bordered by a prominent, crescent-shaped hood, which is strongly inclined toward the edge of the frond. Adjacent “hoods” eventually unite, forming a long colline. No columella. Green polyps on brown background.

**HABITAT.**—Very common on fore-reef slope (25–28 m), particularly in slightly recessed cavities. Also present in sand trough (22 m), inner-reef slope (14–16 m), and high spur and groove zone (6–9 m). Bathymetric range: 3–90 m.

**Family SIDERASTREIDAE**

**Siderastrea siderea (Ellis and Solander, 1786)**

FIGURE 124c; PLATE 5: center left

*Siderastrea siderea*.—Vaughan, 1919:443–447, pl. 114: figs. 2–

3, pl. 122: figs. 1–3.—Roos, 1971:62–63, pl. 13.—Smith, 1971:76–77, pl. 10.—York, 1971:15, pl. 6: figs. 1–2.—Tresslar, 1974:121, pl. 7.—Colin, 1978:232 [color fig.], 235.

Cerioid; encrusting or hemispherical boulders up to 2 m in diameter. Calices 4–5 mm in diameter. Usually more than 48 septa. Inner edges of septa slope gently (about 45°) toward columella, resulting in a wide fossa. Theca fenestrate. Light reddish brown.

**HABITAT.**—Most common in the shallow back-reef area (0.5–2.0 m). Also found on inner-reef slope and patch reefs (Curlew Bank, 6 m). Bathymetric range: 0.5–70.0 m.

**Siderastrea radians (Pallas, 1766)**

FIGURE 124a-b

*Siderastrea radians*.—Vaughan, 1919:439, pl. 114: fig. 1.—

Roos, 1971:62–63, pls. 20–21.—Smith, 1971:76, pl. 9.—York, 1971:15, pl. 6: figs. 3–6.—Werding and Erhardt, 1976, pl. 3: fig. 2.—Colin, 1978:233 [color fig.], 235, 238.

Cerioid; encrusting, hemispherical, or unattached spheroidal colonies rarely exceeding 30 cm in diameter. Unattached coralla with calices covering entire surface. Calices about 3 mm in diameter, 24–40 septa/calice. Inner edges of septa almost vertical, producing a narrow fossa. Theca fenestrate. Greenish or greyish brown.

**HABITAT.**—Most common in the back-reef area (0–20 m), but also collected from the outer fore reef (28 m). Bathymetric range: 0–33 m.

**DISCUSSION.**—Distinguished from *S. siderea* by its smaller size, fewer septa, and vertical, inner septal edges. *S. radians forma stellata* Verrill, a form with a tendency toward deeper calices in a meandriform arrangement, was not collected at Carrie Bow Cay.

**Family PORITIDAE**

**Porites astreoides Lamarck, 1816**

FIGURE 124d; PLATE 2: center right, bottom left  
bottom right

*Porites astreoides*.—Vaughan, 1901:317–318, pls. 32–34.—Verrill, 1901a:160–161, pl. 31: fig. 4.—Squires, 1958:250–

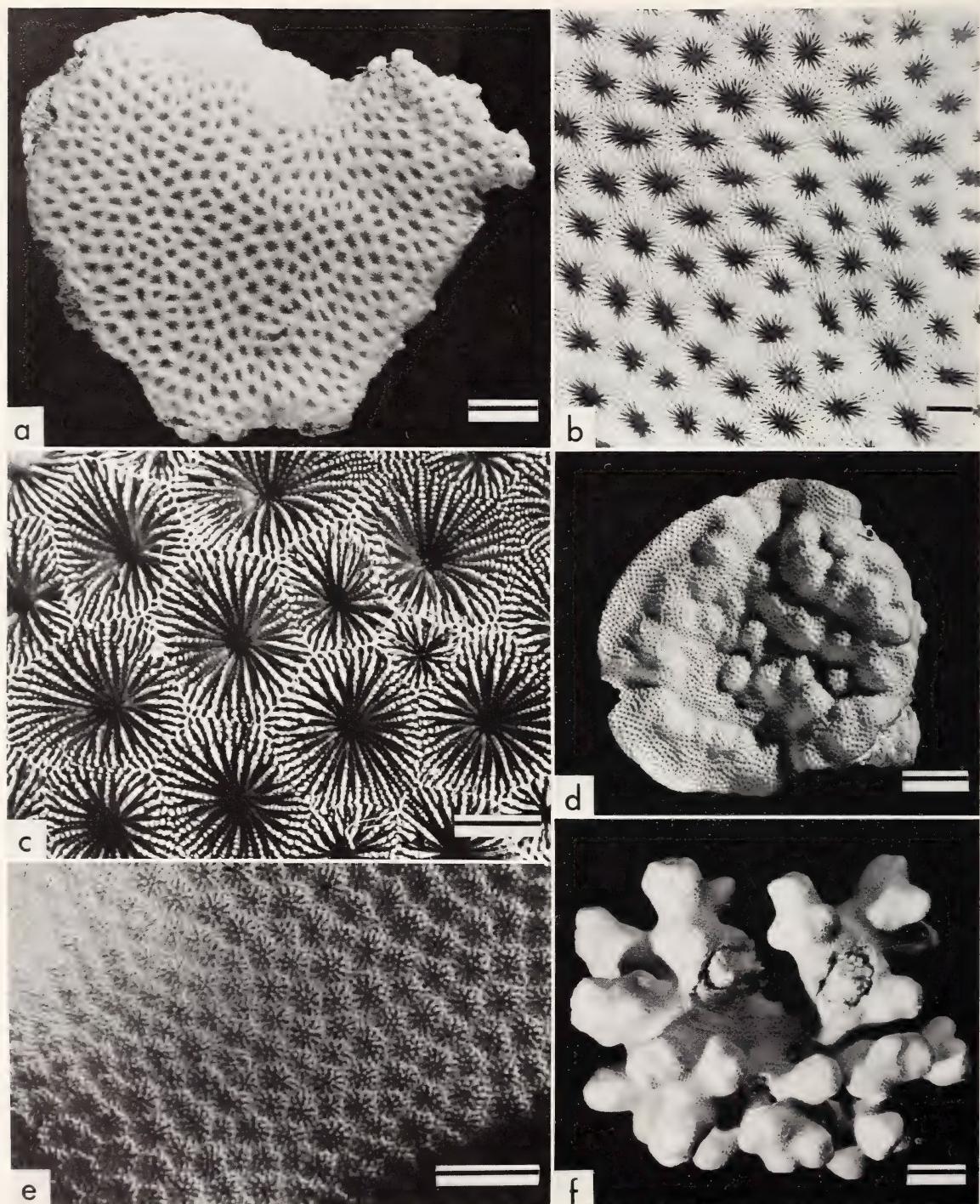


FIGURE 124.—*a, b*, *Siderastrea radians*, exact locality at Carrie Bow Cay unknown; *c*, *S. siderea*, patch reef area, 1 m, specimen coated with NH<sub>4</sub>Cl; *d*, *Porites astreoides*, fore-reef slope, 18 m; *e*, *P. porites f. porites*, exact locality at Carrie Bow Cay unknown; *f*, *P. porites f. porites*, patch reef area, 2-3 m. (Scale bars: *a* = 1 cm; *b, c* = 0.2 cm; *d, f* = 2 cm; *e* = 0.5 cm).

251, pl. 39: figs. 2–3.—Laborel, 1971:187–188, pl. 3: figs. 4–6.—Roos, 1971:61–62, pl. 18: fig. a, pl. 19: fig. a.—Smith, 1971:77, pl. 15.—York, 1971:21, pl. 9: figs. 1–6.—Tresslar, 1974:121, pl. 8.—Erhardt and Meinel, 1975, fig. 1.

*Porites asteroides*.—Colin, 1978:237, 240 [color figs], 242, 243 [figs].

Ceriod; encrusting, flat, or hemispherical colonies rarely exceeding 60 cm in diameter. Surface of colony usually bumpy in shallow-water specimens, flat in deeper-water specimens. Calices 1.25–1.50 mm in diameter, each with 12 septa. Columella small. Bright green or yellowish brown.

**HABITAT.**—Found in all reef environments: back reef (1–2 m), spur and groove zone (6–8 m), sand trough (22 m), and fore-reef slope (18–28+ m). Also known from muddy back reefs and mangrove areas (Roos, 1971). Bathymetric range: 0.2–70.0 m.

### ***Porites porites* (Pallas, 1766)**

FIGURES 124e–f, 125a–c; PLATE 2: top right

*Porites porites*.—Vaughan, 1901:314–316, pl. 2: fig. 4, pls. 28–31.—Squires, 1958:251–253, pl. 38: figs. 1–3, pl. 39: fig. 1.—Roos, 1971:58–60, pls. 16–17.—Smith, 1971:78–79, pls. 13–14.—York, 1971:17, 19, pl. 7: figs. 1–6, pl. 8: figs. 1–5.—Erhardt and Meinel, 1975, fig. 2.—Colin, 1978:236, 237, 239, 243 [color figs].

*Porites polymorpha*.—Verrill, 1901a:158–159, pl. 31: fig. 3.

*Porites*.—Bernard, 1906:5–12, pls. 9–16.

*Porites divaricata*.—Smith, 1971:78.—Colin, 1978:236 [color fig.], 239.

*Porites furcata*.—Smith, 1971:78, pl. 12.—Tresslar, 1974:121, pl. 9.—Colin, 1978:233 [color fig.], 238.

Ceriod, ramose colonies up to 50 cm tall and several meters wide. Branch diameters range from a delicate 5 mm to a massive 25+ mm. Branch tips clubbed or cylindrical, bifurcated or unbranched. Theca porous. Calices 1.5–2.0 mm in diameter, 12 septa/calice. Five-six small pali. Yellow, grey, or buff brown.

**HABITAT.**—*Porites porites* forma *furcata* Lamarck, 1816, is the most common form at Carrie Bow Cay, being found in all reef environments, includ-

ing the lagoon and back reef (1–3 m), the spur and groove zone (7 m), the sand trough (21 m), and the fore-reef slope (27 m). *Forma porites* was observed only in shallow (1–2 m) back-reef areas. *Forma divaricata* Lesueur, 1821, was collected unattached at nearby Twin Cays in a shallow back-reef environment, but not at Carrie Bow Cay. Bathymetric range: 0.5–50 m.

**DISCUSSION.**—There has been continued disagreement on whether the three phenotypes of *Porites porites* are distinct species or simply forms of the same species. Discussions of the problem are found in Vaughan (1901), Bernard (1906), and Roos (1971). This study treats them as formae, owing to the almost continuous range of growth forms shown by the Carrie Bow Cay and other USNM specimens. Traditionally the typical form (sometimes called *P. clavaria* Lamarck, 1816) has thick branches (over 10 mm in diameter) and clavate branch tips; forma *furcata* has branches about 10 mm in diameter, without swollen branch tips; and forma *divaricata* has thin branches (5–6 mm in diameter), which often bifurcate near the tip.

### **Family FAVIIDAE**

#### ***Favia fragum* (Esper, 1797)**

FIGURE 125d

*Favia fragum*.—Vaughan, 1901:303–304, pl. 8.—Squires, 1958:253, pl. 42: fig. 2.—Roos, 1971:68–69, pls. 26–27, pl. 28: fig. a.—Smith, 1971:79–80, pls. 16–17.—York, 1971:21, pl. 9: figs. 7–8.—Colin, 1978:240, 241 [color fig.], 242, 247.

Small, pliocoid, encrusting or hemispherical colonies usually less than 10 cm in diameter. Calices round or irregular in outline; mono-, di-, or tricentric; 5–6 mm in diameter; 36–40 septa/calice. Costae dentate. Columella spongy. Brown or yellow.

**HABITAT.**—Common in shallow lagoonal and back-reef areas (0.5–1 m). Bathymetric range: 0.2–30.0 m.

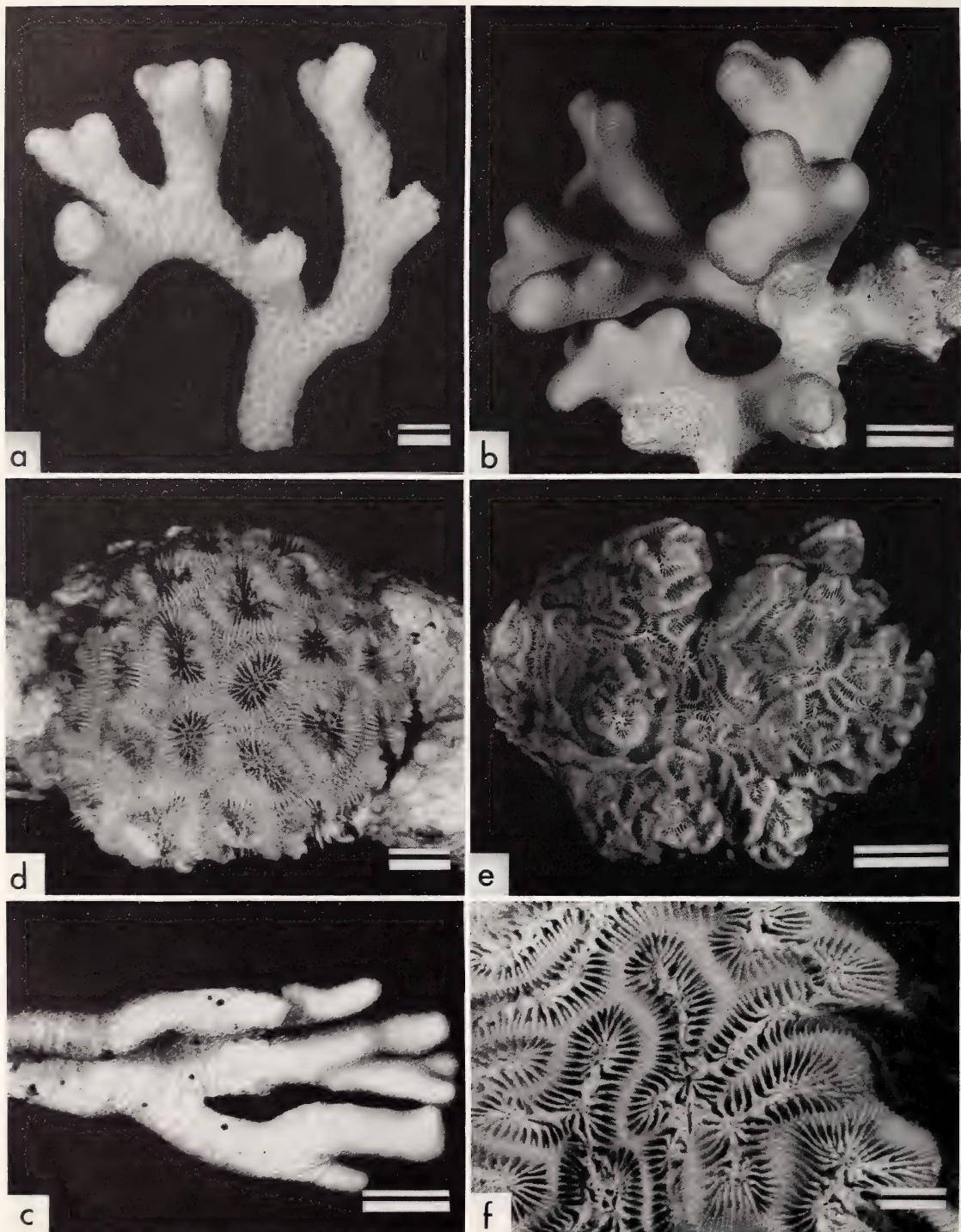


FIGURE 125.—*a*, *Porites porites* f. *divaricata*, Twin Cays, 0.7 m; *b*, *P. porites porites*, same specimen as Figure 124e; *c*, *P. porites furcata*, exact locality at Carrie Bow Cay unknown; *d*, *Favia fragum*, reef crest, 0.5 m; *e*, *f*, *Diploria clivosa*, exact locality at Carrie Bow Cay unknown. (Scale bars: *a*, *d*, *f* = 0.5 cm; *b*, *c*, *e* = 2 cm.)

## *Diploria clivosa* (Ellis and Solander, 1786)

FIGURE 125e-f

*Maeandrina clivosa*.—Matthai, 1928:71–76.

*Diploria clivosa*.—Squires, 1958:253, pl. 42: fig. 2.—Roos, 1971:69–70, pl. 28: fig. b, pls. 30–31.—Smith, 1971:80–81, pls. 19–20.—York, 1971:23, pl. 10: figs. 1–2.—Olivares and Leonard, 1971:56, pl. 3: figs. a–b.—Colin, 1978:244 [color figs.], 250.

Meandroid; encrusting or hemispherical, knobby colonies up to 1 m in diameter. Valleys narrow (3.5–6.0 mm across) and variable in length: usually long but sometimes very short, even monocentric. Septa thin, in two alternate series; 25–38 septa/cm along valley. Principal septa have paliform lobes. Columella spongy. Color variable: yellow, green, bluish, or grey.

**HABITAT.**—Common in lagoon and back-reef areas (0.5–2.0 m). Also present in spur and groove zone (6 m). Bathymetric range: 0–15 m.

## *Diploria strigosa* (Dana, 1848)

FIGURE 126a-b

*Platygyra viridis*.—Vaughan, 1901:306–308, pls. 9–13.

*Maeandrina cerebrum*.—Verrill, 1901a:74–78, pl. 10: fig. 1, pl. 12: fig. 4, pl. 14: figs. 4–5.—Matthai, 1928:55–63.

*Diploria strigosa*.—Squires, 1958:253–254, pl. 42: fig. 1.—Roos, 1971:70–71, pl. 29.—York, 1971:23, pl. 23: figs. 7–8.—Olivares and Leonard, 1971:56, pl. 3: figs. c–d.—Erhardt, 1974, fig. 1c.—Tressler, 1974:122, pl. 10.—Colin, 1978:241 [color fig.], 246 [figs.], 247, 250.

Meandroid; large, hemispherical, evenly convex colonies up to 2 m in diameter. Valleys 6–9 mm across and usually continuous, not short; 15–20 septa/cm, most of which reach columella through paliform lobes. Columella spongy. Dull yellow or greenish brown.

**HABITAT.**—Common in back-reef area (0–2 m) and found once in sand trough of outer fore reef (28 m). Bathymetric range: 0–40 m.

**DISCUSSION.**—*Diploria strigosa* is often confused with *D. clivosa*. The former is distinguished by its even convexity of corallum shape; longer, deeper, and wider valleys; and less numerous septa/cm.

## *Diploria labyrinthiformis* (Linnaeus, 1758)

FIGURE 126c-d

*Meandra labyrinthiformis*.—Verrill, 1901a:70–73, pl. 10: figs. 1, 3.

*Maeandrina labyrinthiformis*.—Matthai, 1928:63–71.

*Diploria labyrinthiformis*: Roos, 1971:71, pl. 32.—Smith, 1971: 81, pl. 21.—York, 1971:23, pl. 10: figs. 3–6.—Erhardt and Meinel, 1975, fig. 6.—Werding and Erhardt, 1976, pl. 2: fig. 1.—Colin, 1978:245 [color figs.], 250–251.

Meandroid; large, hemispherical, evenly convex colonies up to 2 m in diameter. Valleys 5–8 mm across and continuous. Collines grooved by distinct ambulacra. 14–17 septa/cm, most of which reach columella through paliform lobes. Columella spongy. Orange-yellow or brownish yellow.

**HABITAT.**—Common in back-reef area (0.5–2.0 m). Bathymetric range: 0–43 m.

## *Manicina areolata* (Linnaeus, 1758)

FIGURE 126e-f

*Manicina areolata*.—Vaughan, 1901:305, pl. 4: figs. 2–3.—Matthai, 1928:80–91.—Squires, 1958:254–255, pl. 37: figs. 1–3.—Almy and Carrión-Torres, 1963:152–153, pl. 11b.—Roos, 1971:72 pl. 35.—Smith, 1971:83, pls. 25–27.—York, 1971:27, pl. 12: figs. 1–3.—Werding and Erhardt, 1976, pl. 4: fig. 2.—Colin, 1978:248 [color figs.], 251, 254.

*Meandra areolata*.—Verrill, 1901a:81–84, pl. 11: figs. 1–2, pl. 12: figs. 1–3.

*Manicina gyrosa*.—Matthai, 1928:91–95.

*Manicina majori*.—Smith, 1971:83–84.—York, 1971:27, pl. 12: figs. 4–5.

Meandroid colonies consisting of one continuous central valley with numerous side valleys, or a discontinuous series of sinuous valleys. Corallum usually unattached, with a short pedicel or flat base. Collines bear 12–18 septa/cm. Principal septa have large paliform lobes. Columella large and spongy. Yellow to brown, grey, or green.

**HABITAT.**—Forma *areolata* is common in shallow back and patch reefs (York, 1971); however, it was most abundant at Carrie Bow Cay on the outer fore reef (16–27 m). One specimen of forma *majori* Wells, 1936, was collected from the spur and groove zone (10 m). Bathymetric range: 0–65 m.

**DISCUSSION.**—Two forms of this species are rec-

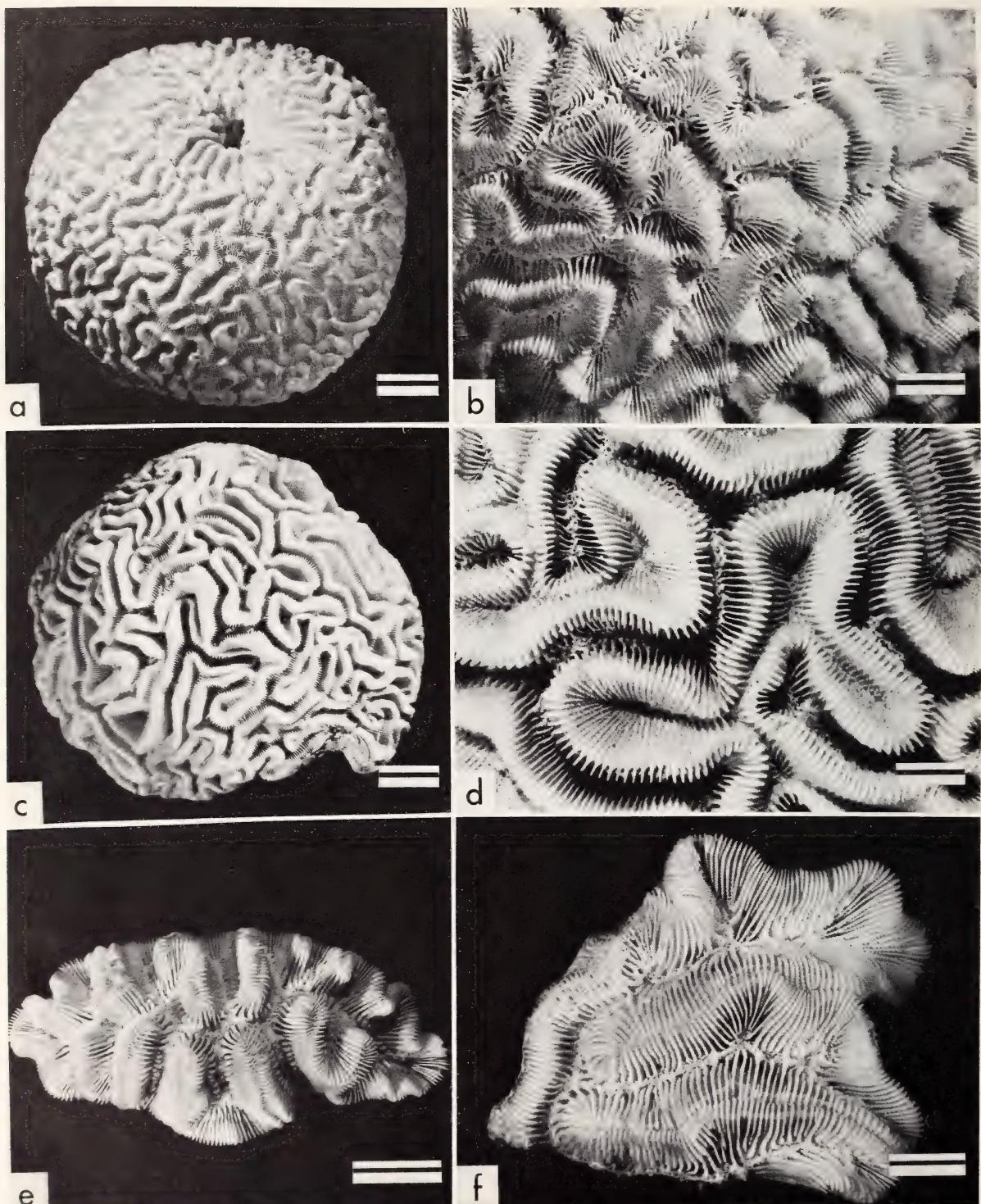


FIGURE 126.—*a, b*, *Diploria strigosa*, exact locality at Carrie Bow Cay unknown; *c, d*, *D. labyrinthiformis*, off Andros, Bahamas; *e*, *Manicina areolata* f. *areolata*, Twin Cays, 1 m; *f*, *M. areolata* *majori*, spur and groove zone. (Scale bars: *a, c, e* = 2 cm; *b, d, f* = 1 cm.)

ognized (Wells, 1973). *Manicina areolata forma areolata* is the smaller form, rarely longer than 15 cm, with one continuous central valley, several side valleys, and generally a short central stalk. *Forma majori* occurs as large (up to 30 cm in diameter), hemispherical boulders, with many sinuous, disconnected valleys and a flat base.

### ***Colpophyllia natans* (Houttuyn, 1772)**

FIGURE 127a-b

*Colpophyllia natans*.—Matthai, 1928:101-107 [not pl. 71: fig. 9, = *C. breviserialis*].—Roos, 1971:73, pl. 33.—Smith, 1971: 82-83, pl. 23.—Wells, 1973, fig. 15.—Colin, 1978:249 [color figs.], 254. [Not York, 1971:25, pl. 11, = *C. breviserialis*.]

Large but light-weight, meandroid colonies up to 1 m in diameter. Valleys long and sinuous, 15-20 mm wide, 10-12 mm deep. Collines bear 8-9 septa/cm. Collines always have two thin parallel ridges. Rudimentary lamellar columella. Green, brown, or yellow.

**HABITAT.**—Common at Carrie Bow Cay: found in back reef (1-2 m), sand trough (22 m), and fore-reef slope (18-27 m). Bathymetric range: 0.5-55.0 m.

**DISCUSSION.**—*Colpophyllia amaranthus* (Houttuyn, 1772) may be a form of *C. natans*. It has been characterized as a smaller, stalked colony with shorter, straight valleys and more septa/cm.

### ***Cladocora arbuscula* (Lesueur, 1821)**

FIGURE 128a

*Cladocora arbuscula*.—Roos, 1971:65, pl. 22: figs. a-b.—Smith, 1971:84, pl. 28.—York, 1971:27 pl. 12: figs. 6-8.—Olivares, 1971:75, pl. 1: figs. a-b.—Colin, 1978:252 [color fig.], 255.

Ramose, bushy, unattached colonies up to 30 cm in diameter. Calices only at ends of branches. Corallites cylindrical, branch and calicular diameters 3-4 mm. Branches distinctly costate. About 36 septa/calice. Columella small and papillose. Brown.

**HABITAT.**—Found only in shallow back-reef *Thalassia* zone (0.5-2.0 m). Bathymetric range: 0.5-21.0 m.

### ***Montastrea annularis* (Ellis and Solander, 1786)**

FIGURE 127c-d; PLATE 4: center left, bottom left, bottom right

*Orbicella acropora*.—Vaughan, 1901:301-302, pls. 6-7.

*Orbicella annularis*.—Verrill, 1901a:94-96, pl. 15: figs. 1-2.—Vaughan, 1919:364-375.

*Orbicella hispidula* Verrill, 1901a:96, pl. 15: figs. 3a-b.

*Montastrea annularis*.—Squires, 1958:256, pl. 40: fig. 3, pl. 41: figs. 1-2.—Roos, 1971:65-66, pl. 24: fig. b, pl. 25: fig. b.—Smith, 1971:85-86, pls. 31-32.—York, 1971:29, pl. 13: figs. 1-8.—Tresslar, 1974:122 pl. 13.—Colin, 1978:230, 243, 253 [color figs.], 258-259.

Massive, plocoid colonies up to 2 m in height or diameter. Shape variable: hemispherical, flat encrusting, platy, or columnar (see Graus and Macintyre, herein: 441). Calices 2-4 mm in diameter; 24 septa/calice, 12 of which reach the well-developed, trabecular columella. Yellowish brown or green.

**HABITAT.**—Very common in all reef environments: back reef (0.3-2.0 m), spur and groove zone (10-18 m), and outer fore reef (16-25 m). Bathymetric range: 0.3-80.0 m.

### ***Montastrea cavernosa* (Linnaeus, 1767)**

FIGURE 127e-f

*Orbicella cavernosa*.—Verrill, 1901a:102-103.—Vaughan, 1919:380-384.

*Montastrea cavernosa*.—Squires, 1958:255-256, pl. 40: figs. 1-2.—Roos, 1971:66-67, pl. 22: fig. c, pl. 23.—Smith, 1971: 86-87, pl. 33.—York, 1971:31, pl. 14: figs. 1-4.—Laborel, 1971:198-200, pl. 5: figs. 2-4.—Tresslar, 1974:122, pl. 14.—Colin, 1978:8 [fig.], 256 [color figs.], 259, 262.

*Montastrea brasiliiana*.—Smith, 1971:86.

Massive, plocoid colonies up to 2 m in diameter. Hemispherical, flat, or encrusting in shape; often with small, irregular knobs. Calices 5-11 mm in diameter; 48 septa/calice, 24 of which reach the well-developed, trabecular columella. Columellar trabeculae usually swirled in clockwise direction. Brown, green, olive, or red.

**HABITAT.**—Common in spur and groove zone (16-20 m) and entire outer fore reef (16-26+ m). Bathymetric range: 0.5-95 m.

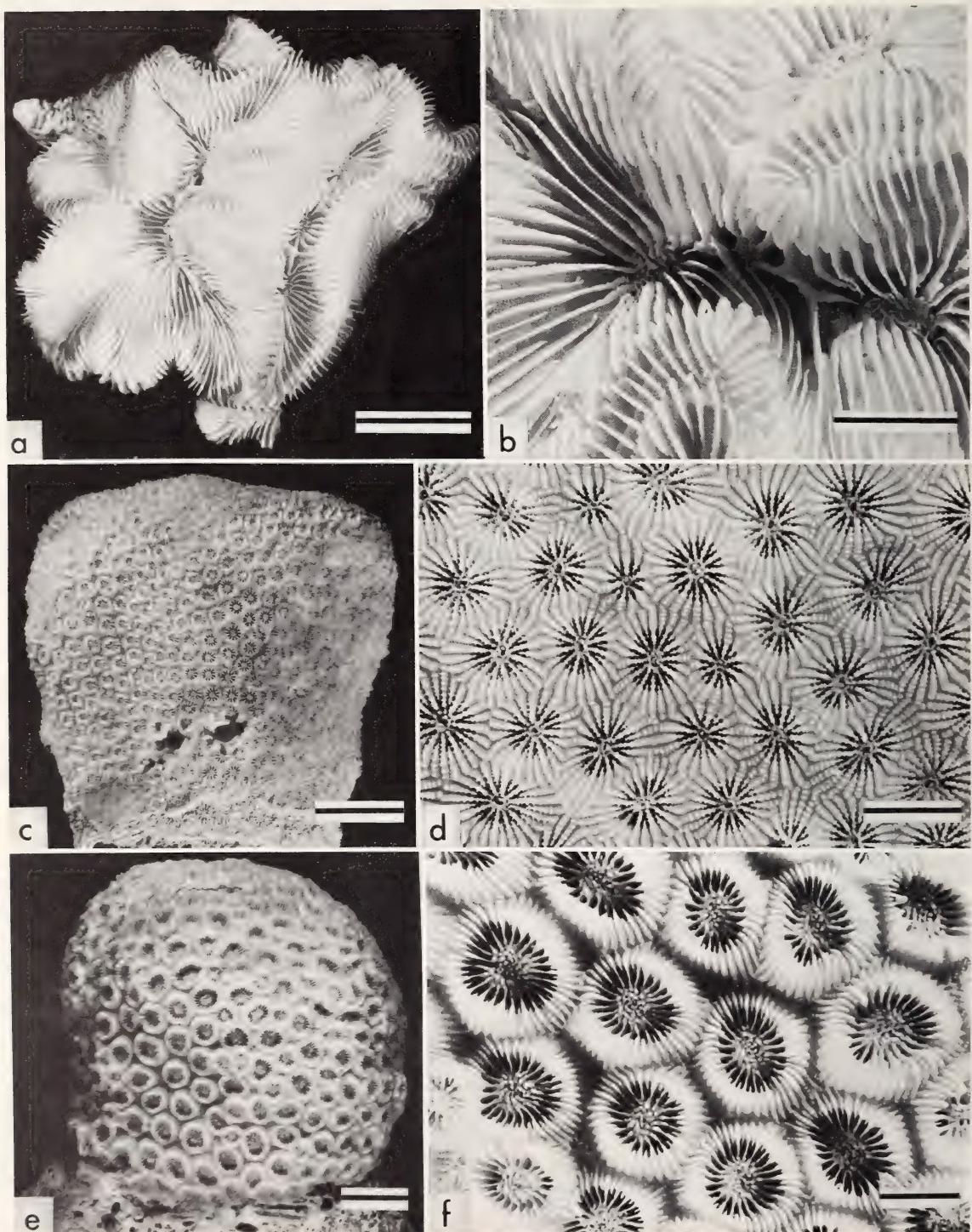


FIGURE 127.—*a, b*, *Colpophyllia natans*, exact locality at Carrie Bow Cay unknown; *c*, *Montastrea annularis*, exact locality at Carrie Bow Cay unknown; *d*, *M. annularis*, fore-reef slope, 24–27 m; *e, f*, *M. cavernosa*, exact locality at Carrie Bow Cay unknown. (Scale bars: *a, c, e* = 2 cm; *b* = 1 cm; *d, f* = 0.5 cm.)

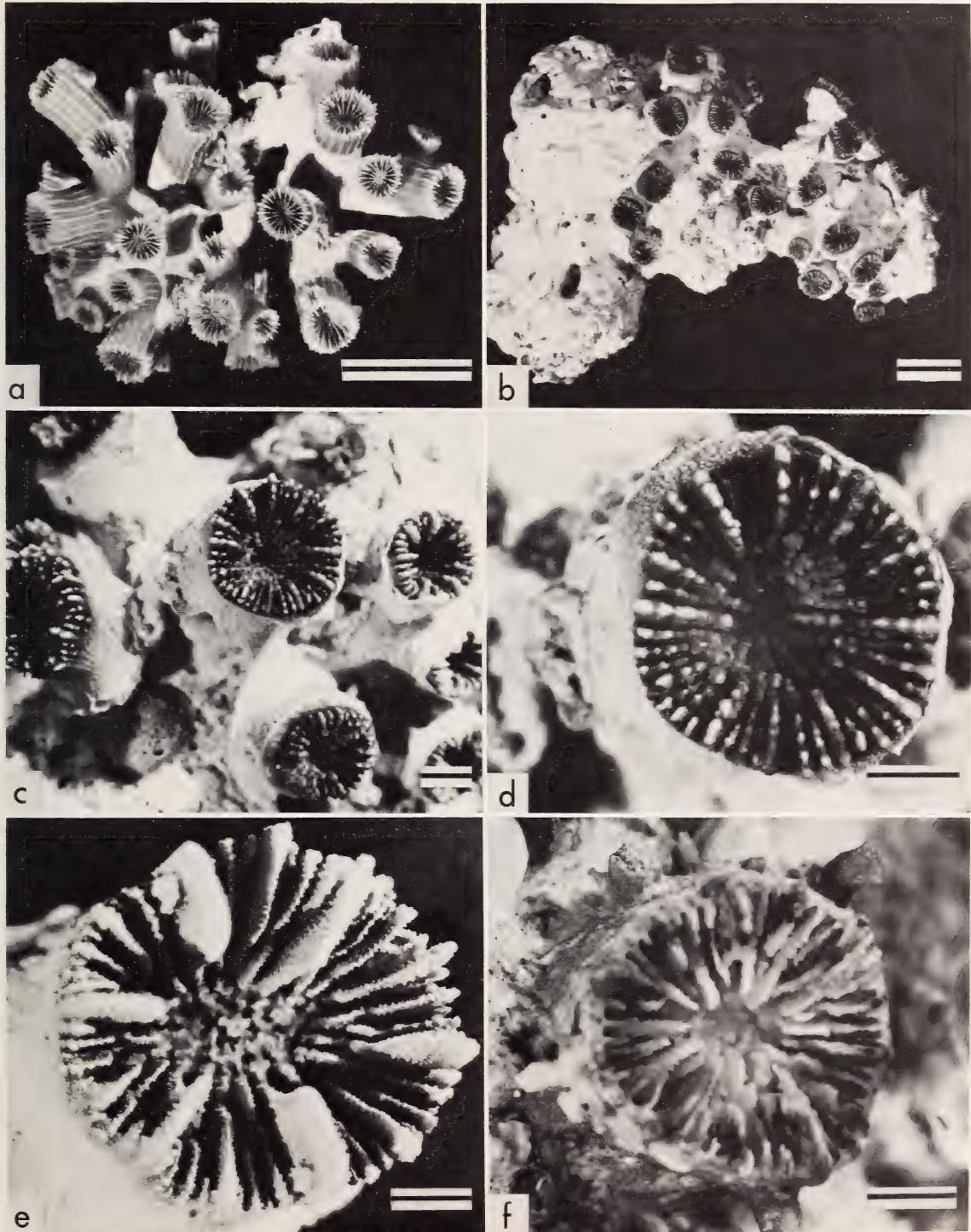


FIGURE 128.—*a*, *Cladocora arbuscula*, Thalassia area, 1 m; *b-d*, *Astrangia solitaria*, Curlew Bank, 6 m; *e*, *Phyllangia americana*, Twin Cays, on a mangrove root, 0.5 m, specimen coated with NH<sub>4</sub>Cl; *f*, *Colangia immersa*, inner reef slope, 16 m. (Scale bars: *a*, *b* = 1 cm; *c-f* = 0.2 cm.)

## Family RHIZANGIIDAE

### *Phyllangia americana* Milne Edwards and Haime, 1849b

FIGURE 128e

*Phyllangia americana*.—Roos, 1971:74, pl. 36.—Smith, 1971: 87–88.—Olivares and Leonard, 1971:64, pl. 8: figs. c–d.—Calin, 1978:257 [color fig.], 262–263.

Small, encrusting colonies that increase by extratentacular budding from edge zone. Corallites cylindrical, about 10 mm in calicular diameter and 10 mm tall. Calices have 36–48 septa with 6–7 highly exsert primaries. Paliform lobes often present on S<sub>3</sub>. Columella rudimentary, spongy. Color of corallum brown.

HABITAT.—Not found at Carrie Bow Cay, but present at Twin Cays (4 km NW of Carrie Bow Cay), encrusting a living *Strombus* gastropod and a mangrove root (0.5–1.0 m). Ahermatypic. Bathymetric range: 0.3–17 m.

### *Astrangia solitaria* (Lesueur, 1817)

FIGURE 128b–d

*Astrangia solitaria*.—Roos, 1971:74, pl. 34.—Smith, 1971: 87.—Wells, 1972:2–4, figs. 1–5.—Colin, 1978:257 [color fig.], 262.

Encrusting colonies that increase by extratentacular budding from basal stolons. Stolons often subsequently obscured, giving the appearance of solitary corallites. Corallites cylindrical, measuring 3–6 mm in calicular diameter, up to 20 mm tall. Calices have 36–48 septa; the fourth cycle is rarely complete. Narrow, multiple paliform teeth on inner edges of all but last cycle of septa. Columella rudimentary, papillose. Corallum brown.

HABITAT.—Cryptic. Found in crevices and on undersides of platy corals or overhangs. Common at Curlew Bank (6 m) and buttress zone (6 m). Ahermatypic. Bathymetric range: 0.2–43 m.

## *Colangia immersa* Pourtales, 1871

FIGURE 128f

Encrusting colonies that increase by extratentacular budding from edge zone. Coenosteum between corallites often obscured, which gives them the appearance of solitary corallites. Corallites cylindrical, measuring 6–8 mm in calicular diameter and up to 10 mm tall. Calices have 36–48 septa with six highly exsert primaries. Well-developed paliform lobes on S<sub>3</sub>. Columella papillose or lamellar. Polyp light green with colorless tentacles. Corallum white, speckled with brown.

HABITAT.—Cryptic. Found rarely on undersides of platy corals on inner reef slope (17 m) and fore-reef slope (26 m). Ahermatypic. Bathymetric range: 3–95 m.

## Family MEANDRINIDAE

### *Meandrina meandrites* (Linnaeus, 1758)

FIGURE 129a–c

*Meandrina brasiliensis*.—Verrill, 1901b:190–192, fig. 14, pl. 34: fig. 1.—Smith, 1971:89–90, pl. 36.

*Meandrina meandrites*.—Vaughan, 1901:296–297, pl. 3, pl. 4: fig. 1, pl. 5.—Roos, 1971:76, pl. 40.—Smith, 1971:89, pl. 35.—Erhardt, 1974, figs. 2–3.—Colin, 1978:261 [color figs.], 263, 264 [color fig.], 266.

*Pectinia meandrites*.—Matthai, 1928:161–166.

*Pectinia brasiliensis*.—Matthai, 1928:167–169.

*Meandrina brasiliensis*.—Laborel, 1971:201–207, figs. 2–5, pl. 6: figs. 3–4.

*Meandrina danae*.—Smith, 1971:90.

This species occurs in three forms. Forma *meandrites* produces massive, meandroid, flat or convex colonies up to 1 m in diameter. The sinuous valleys are long, about 10 mm wide, and continuous. Forma *danae* (Milne Edwards and Haime, 1848), is much smaller (up to 15 cm long), and usually unattached. It has one long, continuous valley, which usually bifurcates at both ends, and smaller, paired valleys projecting perpendicular to the main valley. Forma *brasiliensis* (Milne Edwards and Haime, 1848), is similar to the former but does not have bifurcated valley tips. It is most

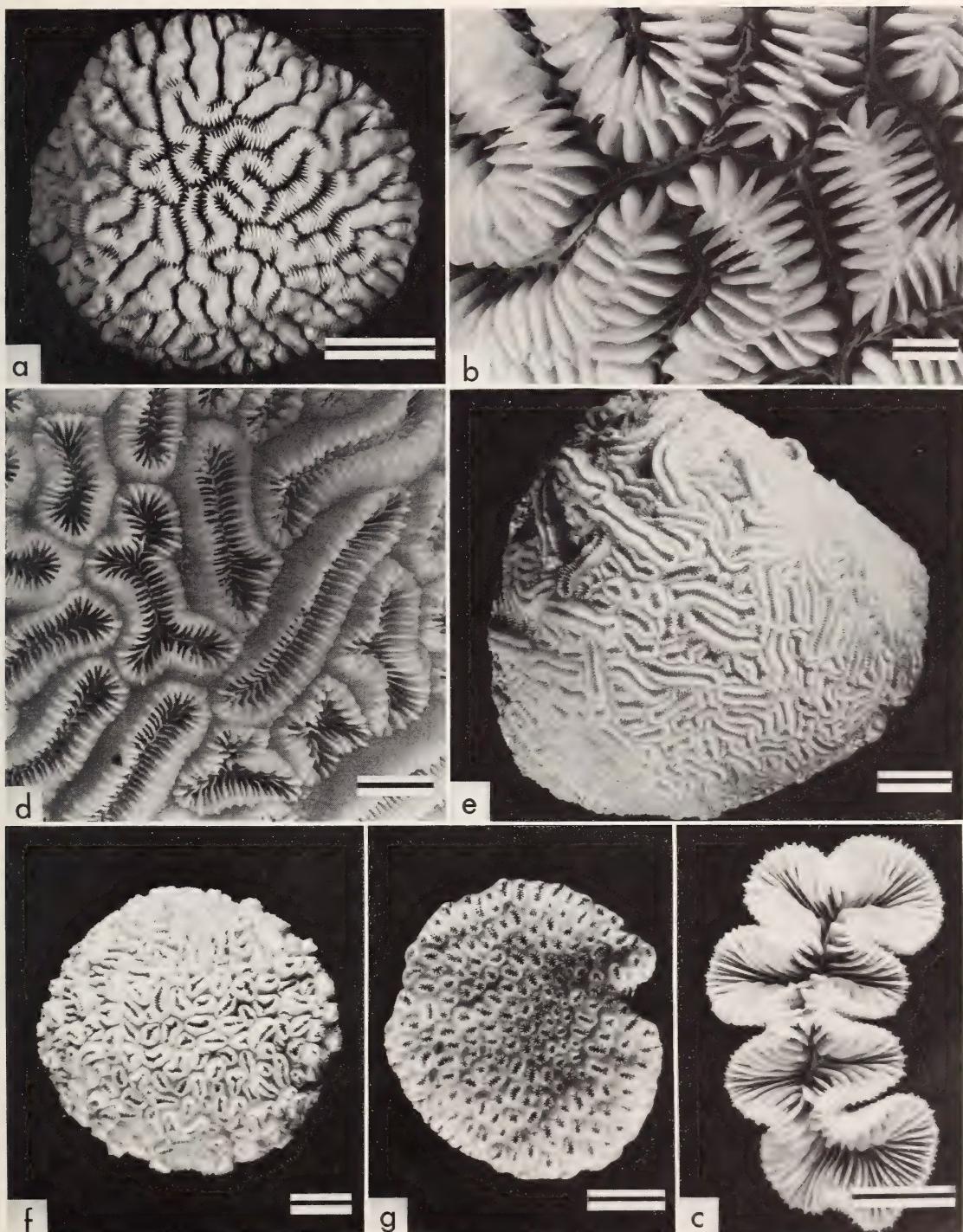


FIGURE 129.—*a, b*, *Meandrina meandrites* f. *meandrites*, exact locality at Carrie Bow Cay unknown; *c*, *M. meandrites* f. *danae*, Wee Wee Cay, 5–6 m; *d, e*, *Dichocoenia stokesi*, patch reef area, 7 m; *f*, *D. stokesi*, exact locality at Carrie Bow Cay unknown, protuberant short calices, "stellaris" form; *g*, *D. stokesi*, fore-reef slope, 30 m, "stellaris" form. (Scale bars: *a* = 5 cm; *b, e* = 0.5 cm; *c–g* = 2 cm.)

common off Brazil. All forms have 6–8 wide primary septa per cm alternating with smaller septa. Columella lamellar. Brown to yellow.

**HABITAT.**—*Forma meandrites* is very common on the outer fore reef, especially the fore-reef slope (22–40 m). It also occurs in the spur and groove zone (6–8 m) and at adjacent patch reefs (7 m). *Forma danae* was not seen at Carrie Bow Cay but was collected at Wee Wee Cay (11 km SW of Carrie Bow Cay) in a *Thalassia* area (4–6 m). *Forma brasiliensis* was not collected at Carrie Bow Cay. Bathymetric range 0.5–80 m.

**DISCUSSION.**—*Meandrites meandrites forma danae* bears the same morphological relationship to the typical form as *Manicina areolata forma areolata* bears to *M. areolata forma majori*. The three forms of *M. meandrites* are often considered as separate species.

### *Dichocoenia stokesi* Milne Edwards and Haime, 1848

FIGURE 129d–g

*Dichocoenia stokesii*.—Mathai, 1928:198–201.—Squires, 1958: 257, pl. 34: fig. 4.—Roos, 1971:77–78, pls. 41–43.

*Dichocoenia stellaris*.—Mathai, 1928:201, pl. 63: fig. 2.—Wells, 1973:45–47, figs. 31–33.—Colin, 1978:267, 268 [color fig.].

*Dichocoenia stokesi*.—York, 1971:33, pl. 15: figs. 1–4.—Wells, 1973:44–45, figs. 29–30.—Colin, 1978; 265 [color figs.], 266–267, 268 [color fig.].

Placoid to meandroid, flat or convex colonies up to 50 cm in diameter. Calices monocentric or polycentric in valleys up to 50 mm long, 3–5 mm wide. Costae absent or very short; intercalicular surface spinose. Small paliform lobes commonly present on principal septa. Columella rudimentary, varying from spongy to lamellar. Yellow, brown, or green.

**HABITAT.**—Common in most reef environments: patch reefs (5–7 m), spur and groove zone (9–10 m), and outer fore reef (18–31 m). Bathymetric range: 2–72 m.

**DISCUSSION.**—*Dichocoenia stellaris* Milne Edwards and Haime, 1848, is considered a distinct species by some authors on the basis of its flat growth form and short, nonmeandrine calices.

My examination of the Carrie Bow Cay specimens and additional specimens in the USNM collection and at the University of Miami revealed all intergrades of corallum shape (flat to spherical) and valley length. I see no reason for maintaining them as separate species based on skeletal characters.

### *Dendrogyra cylindrus* Ehrenberg, 1834

FIGURE 130a–b

*Dendrogyra cylindrus*.—Matthai, 1928:170–171.—Roos, 1971: 76–77, pls. 38–39.—Smith, 1971:90–91, pls. 38–39.—York, 1971:33, pl. 15: figs. 5–8.—Colin, 1978: 269 [color figs.], 270, 271 [fig.], 274 [fig.].

Meandroid colonies forming vertical pillars up to 3 m tall. Valleys sinuous, narrow (3–4 mm), and discontinuous. Collines have 7–10 thick, non-dentate septa/cm. Collines broad with grooved ambulacra; ambulacrum rudimentary or absent toward top of pillar. Columella lamellar and discontinuous. Dark brown.

**HABITAT.**—Rare at Carrie Bow Cay. Collected only in spur and groove zone (14 m) and back reef (1 m). Bathymetric range: 1–20 m.

## Family MUSSIDAE

### *Mussa angulosa* (Pallas, 1766)

FIGURE 130c–d

*Mussa angulosa*.—Matthai, 1928:204–208 [not pl. 64: fig. 2, pl. 68: fig. 2].—Roos, 1971:79–80, pls. 45–46.—Smith, 1971:92, pl. 42 [not pl. 41].—Tresslar, 1974:123, pl. 15.—Colin, 1978:270, 272 [color figs.], 275.

Large, phaceloid to meandroid-phaceloid colonies with branch diameters up to 5 cm. Calices occur at ends of branches; mono- to polycentric (up to four centers) with trabecular linkage. Costae dentate near calice, often forming long, thin, raised ridges toward base. Septa coarsely dentate. Trabecular columella well developed. Large, fleshy polyps; pink, purple, brown, or green.

**HABITAT.**—Rare at Carrie Bow Cay. Found on inner-reef slope (21 m) and fore-reef slope (17–26 m). Bathymetric range: 1.5–59 m.

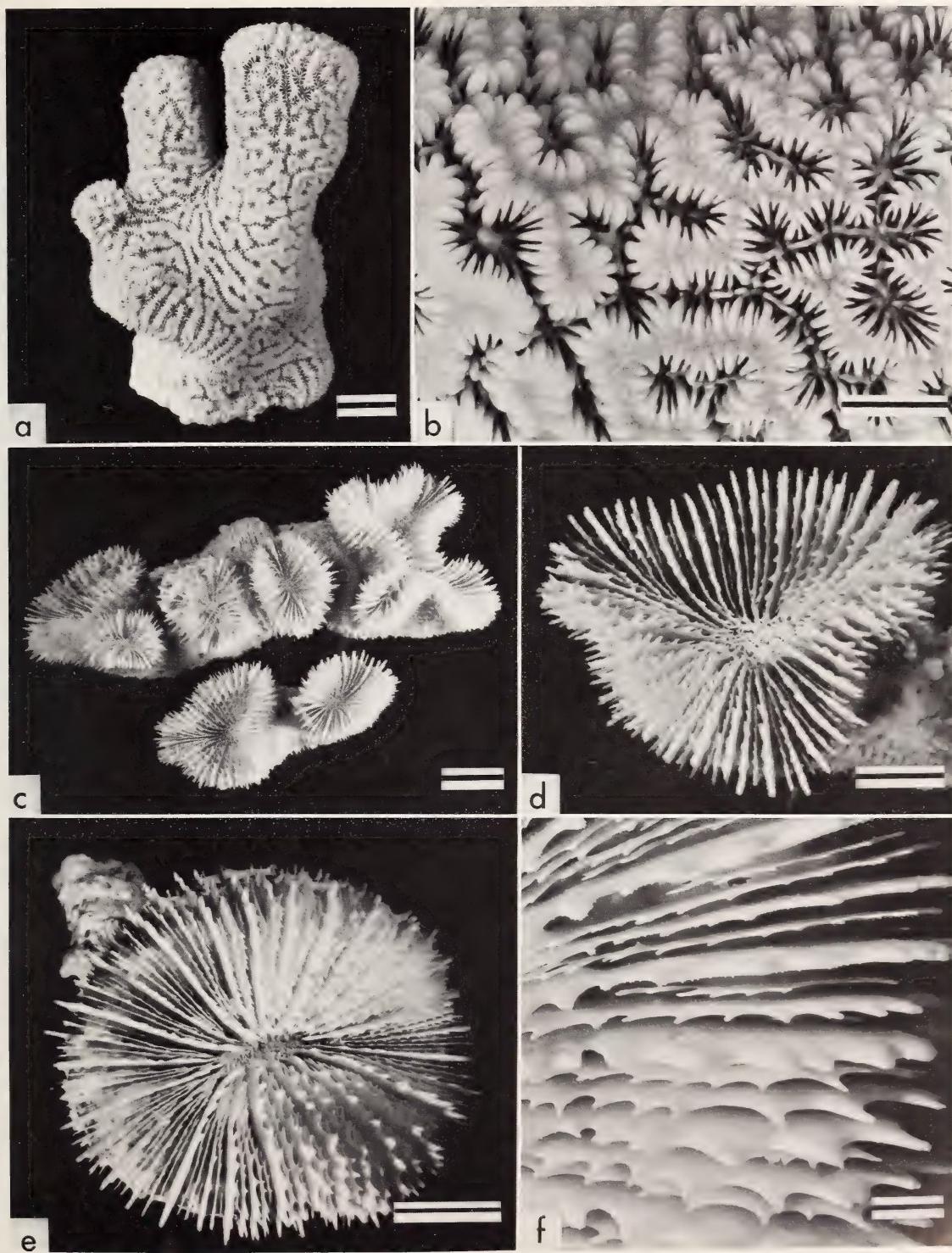


FIGURE 130.—*a, b*, *Dendrogyra cylindrus*, 14 m; *c, d*, *Mussa angulosa*, inner reef slope, 21 m; *e, f*, *Scolymia lacera*, fore-reef slope, 20–28 m. (Scale bars: *a, c, e* = 2 cm; *b, d* = 1 cm; *f* = 0.5 cm.)

***Scolymia lacera* (Pallas, 1766)**

FIGURE 130e-f

*Scolymia lacera*.—Wells, 1964:381–382, pl. 22: figs. 5–6.—Roos, 1971:78–79, pl. 44.—Smith, 1971:92, pl. 41.—Lang, 1971:952–957, figs. 1–2.—Wells, 1971:960–963, figs. 1, 2, 4, 6.—Laborel, 1971:220, pl. 7: fig. 6.—Colin, 1978:273–274 [figs.], 275, 278.

Solitary, subcylindrical, firmly attached coralla up to 15 cm in diameter (but more often 5–6 cm). Calice round to elliptical in outline. Up to six cycles of septa; last cycle usually incomplete. Septa of first three cycles larger and more exsert than others. Septa coarsely dentate, less than five triangular teeth/cm. Costae dentate like septa. Columella large, elongate, trabecular. Polyps large and fleshy; green, brown, or red.

HABITAT.—Common on the fore-reef slope (14–40 m) and sand trough of outer fore-reef (21 m). Bathymetric range: 14–80 m.

***Scolymia cubensis* (Milne Edwards and Haime, 1849a)**

FIGURE 131a-b

*Scolymia cubensis*.—Lang, 1971:952–957, 2 figs.—Wells, 1971:960–963, figs. 1, 3, 5, 7.—Tresslar, 1974:123, pl. 16.—Colin, 1978:273, 276 [color figs.], 278.

Solitary, subcylindrical, firmly attached coralla up to 10 cm in diameter. Up to six cycles of septa, last cycle incomplete. Septa finely dentate with at least five tall, attenuated teeth/cm. Costae also dentate. Columella large, trabecular. Dark brown.

HABITAT.—Found only on fore-reef slope (30–40 m). Bathymetric range: 20–80 m.

DISCUSSION.—*Scolymia cubensis* is distinguished from the very similar *S. lacera* by its finer septal dentition and its less exsert and thinner S<sub>1–3</sub>. A third similar species, *S. wellsii* Laborel, 1967, is distinguished by its very tall, laciniate septal dentition. Small coralla (smaller than 3 cm) of all three species are difficult to distinguish.

***Isophyllum sinuosa* (Ellis and Solander, 1786)**

FIGURE 131c-d

*Isophyllum dipsacea*.—Verrill, 1901a:118–121, pl. 18: fig. 2, pl. 19: figs. 2, 3, pl. 20: fig. 2.

*Isophyllum fragilis*.—Verrill, 1901a: 121–125, pl. 16: figs. 1, 2, pl. 17: figs. 1–7, pl. 18: fig. 1, pl. 19: figs. 1, 4, 5.

*Isophyllum sinuosa*.—Matthai, 1928:237–247.—Squires, 1958: 257–258, pl. 40: fig. 4.—Roos, 1971:81, pls. 48, 50.—Smith, 1971:94, pl. 46.—York, 1971:39, pl. 18: figs. 1–3.—Colin, 1978:276–277 [color figs.], 279.

Medium size, meandroid colonies up to 20 cm in diameter. Valleys short (monocentric) or long and sinuous; 20–25 mm across. Collines tall and narrow, often ridged. About 7–9 septa/cm, the 4–5 principal septa reaching the columella. Septa bear sharp, attenuated teeth. Columella and calicular linkages trabecular. Variegated, lavender, brown, green, yellow.

HABITAT.—Very common in back reef (1–2 m); also found in sand trough of outer fore reef (28 m). Previously known bathymetric range: 1–10 m.

DISCUSSION.—*Isophyllum multiflora* Verrill, 1901a, has been considered a distinct species by some authors because of its (1) smaller corallum, (2) narrower valleys, and (3) larger number of septa/cm. I consider these characteristics to be within the range of variation of *I. sinuosa*, therefore *I. multiflora* was not distinguished in this report.

***Isophyllastrea rigida* (Dana, 1848)**

FIGURE 131e-f

*Mussa rigida*.—Verrill, 1901a:127–128, pl. 25: figs. 2–3, pl. 33: fig. 4.

*Isophyllastrea rigida*.—Matthai, 1928:263–268, pl. 54: fig. 3, pl. 57, figs. 2–3.—Squires, 1958:258, pl. 41: fig. 3.—Roos, 1971:80–81, pl. 47.—Smith, 1971:92–93, pl. 43.—York, 1971:35, pl. 16: figs. 1–6.—Colin, 1978:279, 280 [color fig.], 282.

Cerioid, attached, flat to hemispherical colonies up to 15 cm in diameter. Calices mono-, di-, or tricentric; polygonal or irregular in shape. A monocentric calice about 10 mm in diameter contains 25–30 septa. Coarsely dentate septa. Ru-

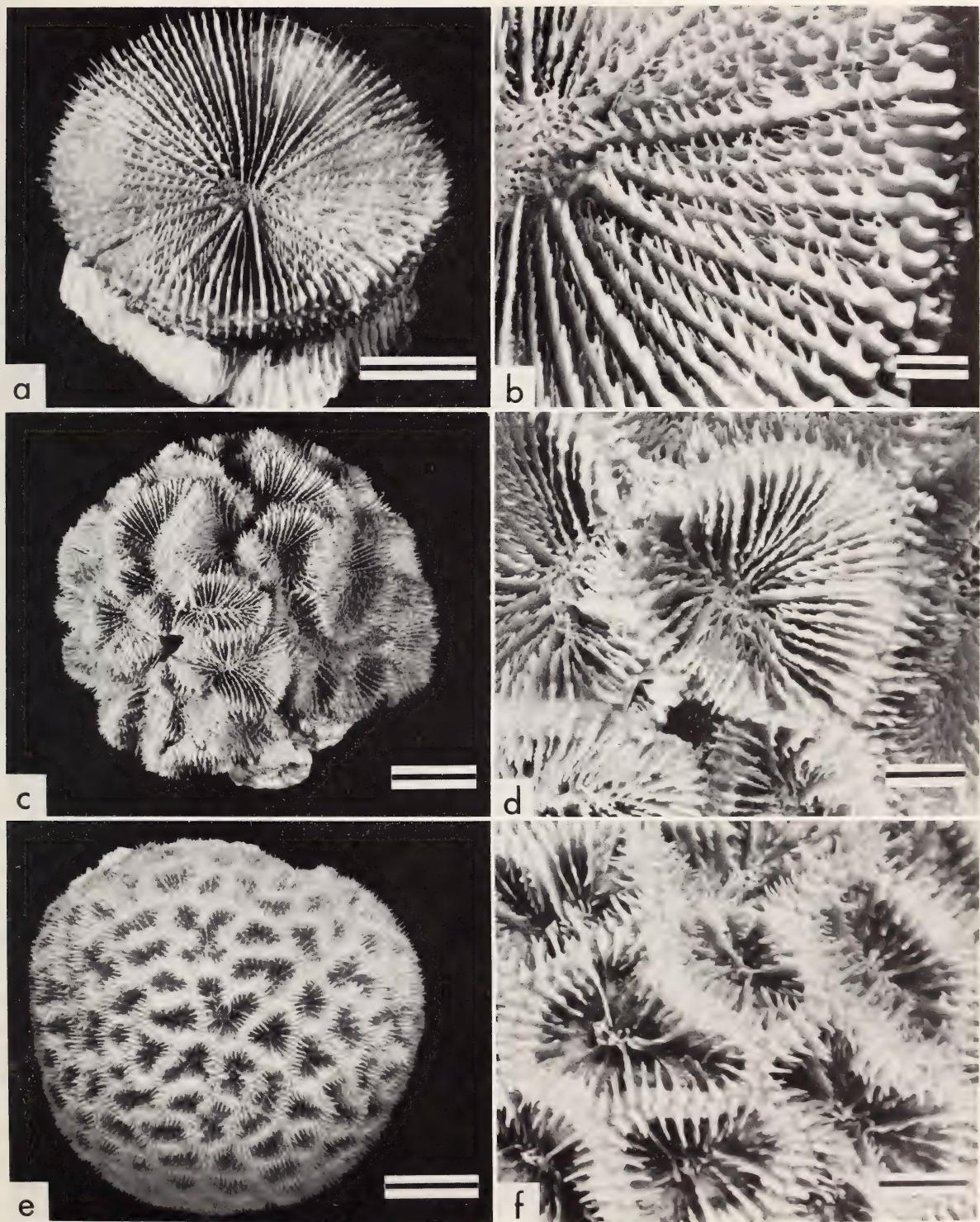


FIGURE 131.—*a, b*, *Scolymia cubensis*, fore-reef slope, 39 m; *c, d*, *Isophyllia sinuosa*, 2 m; *e, f*, *Isophyllastrea rigida*, upper spur and groove zone, 6 m. (Scale bars: *a, c, e* = 2 cm; *b, d, f* = 0.5 cm.)

dimentary columella, composed of loose trabeculae. Green, pinkish, or purple.

**HABITAT.**—Common in spur and groove zone (6–8 m). Also found in back reef (2 m) and fore-reef slope (20 m). Bathymetric range: 1–20 m.

### ***Mycetophyllia lamarckiana* Milne Edwards and Haime, 1848**

FIGURE 132e

*Mycetophyllia lamarckiana*.—Matthai, 1928:250–255 [in part].—Smith, 1971:93–94, pl. 44 [not pl. 45 = *M. ferox*].—Wells, 1973:38, fig. 16.—Colin, 1978:280–281 [color figs.], 282.

Not *Mycetophyllia lamarckiana*.—Roos, 1971:82, pls. 49, 51 [= *M. ferox*].—York, 1971:37, pl. 17: figs. 1–7 [= *M. ferox* and ?*M. danaana*].

Medium size (up to 12 cm in diameter), weakly attached, often turbinate colonies with a nearly circular calicular surface. The central, founder polyp is surrounded by a ring of 7–10 polyps budded circumorally. Subsequently each marginal polyp forms a chain of polyps intramurally, a colline forming between each chain. A chain may split, in which case a new colline is added. Continuous valleys, 10–20 mm wide, all radiate from the central polyp. Septa coarsely dentate. Direct lamellar linkage. Rudimentary columella. Green, brown, or grey.

**HABITAT.**—Not common at Carrie Bow Cay: found in spur and groove zone (6–8 m) and fore-reef slope (27 m). Bathymetric range: 3–60 m.

**DISCUSSION.**—Several specimens kept alive for several days revealed a complete absence of polyp tentacles but a distinct submarginal row of tentacles, one corresponding to each septum. These short tentacles, recessed in a continuous groove 3–5 mm from the edge of the corallum, immobilized and transferred prey to the oral surface (coenosarc) where it was then transported to an adjacent stomodeum. Lack of polyp tentacles has been reported for *Mycetophyllia reesi* Wells, 1973, but this is the first report of a ring of submarginal tentacles for Scleractinia.

### ***Mycetophyllia aliciae* Wells, 1973**

FIGURES 132f, 133a–b

*Mycetophyllia aliciae* Wells, 1973:41–43, figs. 25–28.—Colin, 1978:283 [figs.], 285 [color figs.], 286 [fig.], 287, 290.

Thin, platy, weakly attached colonies forming nearly circular calicular surfaces up to 30 cm in diameter. Circumoral budding followed by intra-mural budding. Radiating, low collines, often discontinuous, flanking wide valleys (20–80 mm) of 1–5 rows of calices. Collines may be absent. Thick, coarsely dentate septa; 7–12/calice. Inner edges of septa usually elevated adjacent to calicular fossa. Direct lamellar linkage. Columella absent. Greyish brown, greenish brown, or green.

**HABITAT.**—Collected only on fore-reef slope (25 m). Bathymetric range: 18–75 m.

**DISCUSSION.**—*Mycetophyllia aliciae* resembles *M. lamarckiana* in its similar mode of intratentacular budding. The former is distinguished by its thicker septa, wider valleys, larger corallum, and lack of columella.

### ***Mycetophyllia danaana* Milne Edwards and Haime, 1849a**

FIGURE 132a–c

?*Mycetophyllia lamarckiana*.—York, 1971:37, pl. 17: figs. 1–4.

*Mycetophyllia danaana*.—Wells, 1973:38, figs. 17–18.—Colin, 1978:281 [color fig.], 287.

Massive, weakly attached, irregularly-shaped, meandroid colonies up to 35 cm in diameter. Founder polyp (calice) usually not apparent. Sinuous valleys long and continuous, 8–17 mm wide. Valleys usually deep (10–15 mm) but may be shallow (4 mm). Coarsely dentate septa. Collines sometimes discontinuous or hydnophoroid. Direct lamellar linkage. Columella rudimentary or absent. Variable in color; often dark green valleys with reddish brown collines. Also pale green, grey, and brownish yellow.

**HABITAT.**—Very common in all areas of outer fore reef (16–27 m); also collected from spur and groove zone (6–8 m). Bathymetric range: 3–30 m.

**DISCUSSION.**—*Mycetophyllia danaana* can easily be

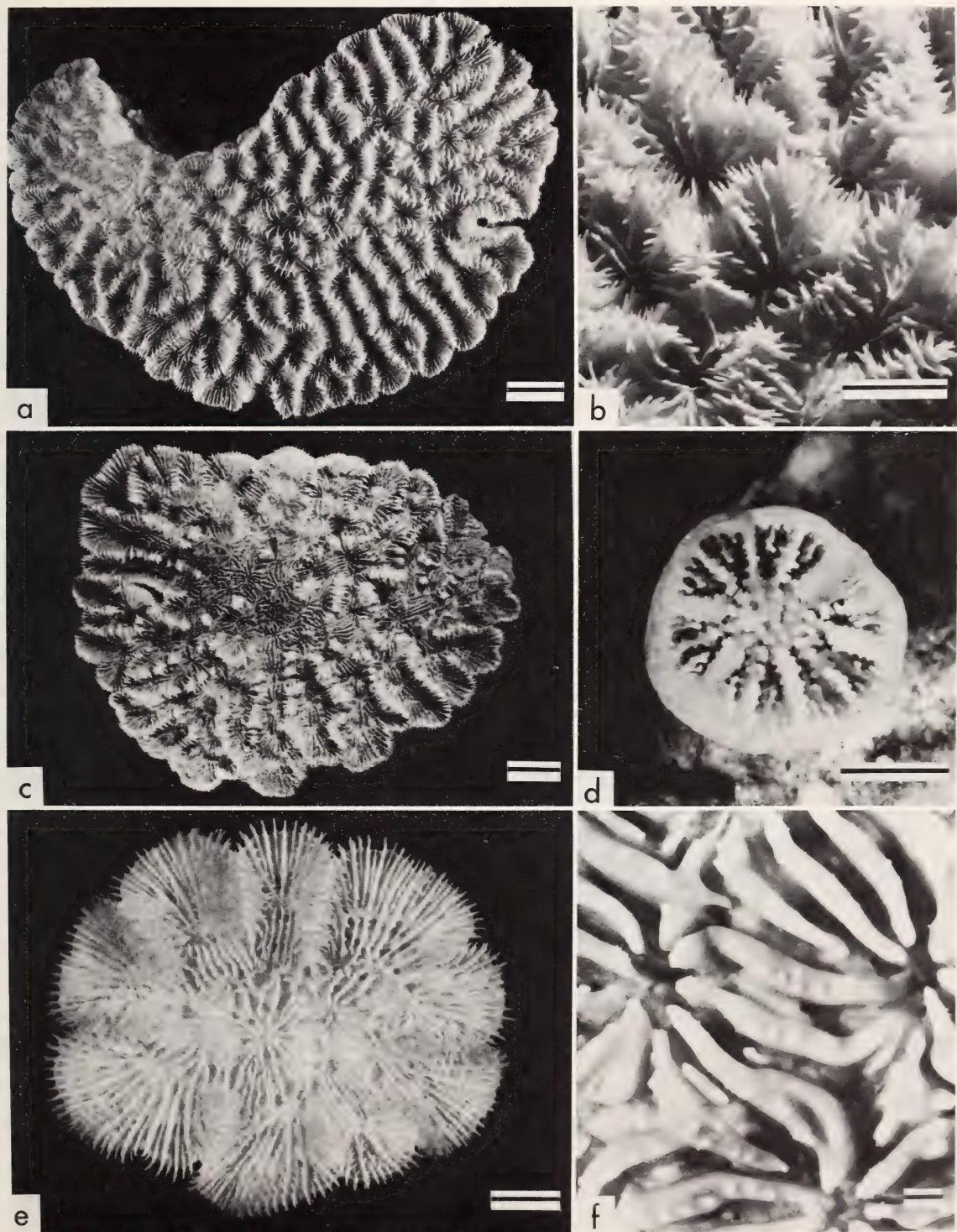


FIGURE 132.—*a, b*, *Mycetophyllia danaana*, fore-reef slope, 24–27 m; *c*, *M. danaana*, fore-reef slope, 16 m, hydrophoroid specimen; *d*, *Gardineria minor*, fore-reef slope; *e*, *M. lamarckiana*, fore-reef slope, 24–27 m; *f*, *M. aliciae*, fore-reef slope, 20–28 m. (Scale bars: *a, c* = 2 cm; *b, e* = 1 cm; *d, f* = 0.2 cm.)

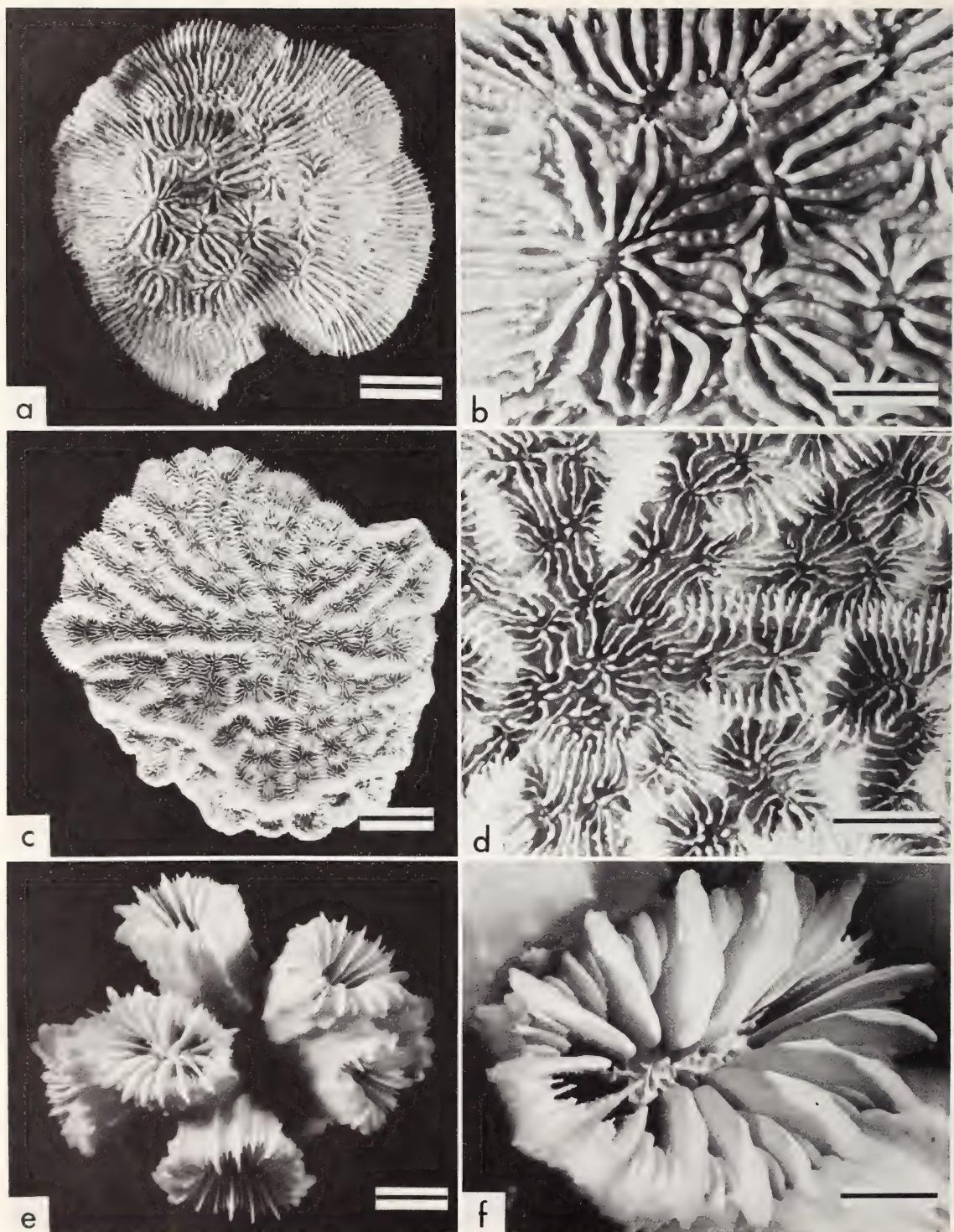


FIGURE 133.—*a, b*, *Mycetophyllia aliciae*, same specimen as Figure 132 *f*; *c, d*, *M. ferox*, fore-reef slope, 17 m; *e, f*, *Eusmilia fastigiata*, spur and groove zone, 10 m. (Scale bars: *a, c* = 2 cm; *b, d*, *e* = 1 cm; *f* = 0.5 cm.)

confused with *M. ferox*, especially the shallow valley forms of *M. danaana*. It is distinguished by its continuous, wider valleys and its more widely spaced calices (usually more than 10 mm apart). The characters of valley depth and number of septa/calice (see Wells, 1973:38) are not reliable to distinguish the species.

### ***Mycetophyllum ferox* Wells, 1973**

FIGURE 133c-d

*Mycetophyllum lamarckiana*.—Roos, 1971:82, pls. 49, 51.—York, 1971: 37, pl. 17, figs. 5-7.

*Mycetophyllum lamarckiana*.—Smith, 1971: 93-94, pl. 45.

*Mycetophyllum ferox* Wells, 1973:40-41, figs. 22-24.—Werding and Erhardt, 1976, pl. 3: fig. 1.—Colin, 1978:284 [color fig.], 286 [fig.], 287.

Meandroid, weakly attached colonies nearly circular in outline and up to 35 cm in width. Founder polyp (calice) usually not evident. Valleys shallow, usually less than 10 mm in width, and sometimes discontinuous: short segments completely enclosed by collines. Septa coarsely dentate. Direct lamellar linkage. Columella rudimentary or absent. Brown or green.

HABITAT.—Rare at Carrie Bow Cay: one specimen collected from fore-reef slope (17-18 m). Bathymetric range: 10-35 m.

DISCUSSION.—See discussion of *M. danaana*.

Small colonies of *Mycetophyllum* are generally difficult to identify because the pattern of their intratentacular budding is not yet established. More specimens and analyses are necessary in order to distinguish the valid species and/or drop the current species to the status of forma. Characteristics of the soft parts, such as tentacle arrangement, may be of taxonomic value. Color does not seem to be a reliable character.

### **Family CARYOPHYLLIIDAE**

#### ***Eusmilia fastigiata* forma *fastigiata* (Pallas, 1766)**

FIGURE 133e-f

*Eusmilia fastigiata*.—Matthai, 1928:190-196.—Roos, 1971: 83, pl. 52.—Smith, 1971:95, pl. 48.—York, 1971:41, pl.

19: figs. 1-6.—Wells, 1973:49, fig. 34a.—Colin, 1978:289 [color fig.], 291, 292 [color figs.].

Phaceloid to phaceloflabellate, bushy colonies up to 50 cm in diameter. Corallites usually mono-, di-, or tricentric but may produce even longer, polycentric series up to 15 cm long. Calices terminal. An average monocentric calice measures 13 × 19 mm in calicular diameter with 72 septa, 14 much larger and more exsert than the others. Ridged costae correspond to the exsert septa. Septal edges smooth. Columella large, composed of twisted trabeculae. Brown, green, or yellow.

HABITAT.—Most common in spur and groove zone (6-10 m) but also found on sand trough of outer fore reef (21 m). Bathymetric range: 1-65 m.

DISCUSSION.—Forma *flabellata* Wells, 1973, distinguished by its long, polycentric series, which produce flabellate branches, was not found at Carrie Bow Cay.

### **Family FLABELLIDAE**

#### ***Gardineria minor* Wells, 1973**

FIGURE 132d

*Gardineria minor* Wells, 1973:49-53, fig. 36a-g.

Solitary, subcylindrical, firmly attached. Calices round, 4-7 mm in diameter. Theca smooth, no costae. Four complete cycles of septa. Inner edges of  $S_1$  smooth; higher cycle septa dentate to laciniate. Paliform lobes usually present before  $S_2$ . Columella papillose.

HABITAT.—Cryptic, but common on undersides of platy corals (for example, *Agaricia*) on fore-reef slope (18-27 m). Ahermatypic. Bathymetric range: 2-241 m.

### **Conclusions**

Thirty-seven species of hermatypic Scleractinia are reported in this paper. In addition, five ahermatypic species found at Carrie Bow Cay bring the total number of Scleractinia for this cay to 42. In comparison, species records of hermatypic corals from other areas of the Caribbean include

46 from Jamaica (Wells, 1973), 41 from Panama (Porter, 1972), 40 from Bonaire (Scatterday, 1974), 38 from Ceycen Island, Colombia (Erhardt and Meinel, 1975), and 37 from Bahia Concha, Colombia (Erhardt, 1974). (These totals have been revised in accord with the systematic approach of this paper.)

The known distribution of corals in western Atlantic reefs suggests that habitats not sampled in the study area may support other species. For example, *Mycetophyllia reesi* Wells, 1973, and at least two species of *Agaricia* may exist in the deeper fore-reef slope (30–70 m), while more intensive collecting in shallow depths may disclose the presence of *Porites branneri* Rathbun, 1888. In fact, two species of hermatypes known previously from Belize were not collected in this study: *Colpophyllia breviserialis* Milne Edwards and Haime, 1849a (reported as *C. natans* by York,

1971, pl. 11: figs. 4–6) and *Oculina diffusa* Lamarck, 1816 (unreported record in USNM collections), bringing the total to 39 hermatypes known from Belize. In addition to the five ahermatypes known from Carrie Bow Cay, five more have been reported from Belize: *Oculina valenciennesi* Milne Edwards and Haime (reported by York, 1971); *Caryophyllia ambrosia* Alcock and *Deltocyathus agassizii* Pourtales (= *Deltocyathus italicus* Mitchellotti) (reported by Boone, 1928); *Deltocyathus moseleyi* Cairns and *Javania cailleti* (Duchassaing and Michelotti) (reported by Cairns, 1979). Thus, the scleractinian fauna of Belize totals 49 species, of which 39 are hermatypic and 10 are ahermatypic.

Calcified hydrozoans, commonly listed as part of a stony coral fauna, were also found during this study: two species of Milleporina and one representative of Stylasterina.

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# Octocorallia (Cnidaria) from Carrie Bow Cay, Belize

Katherine Muzik

## ABSTRACT

At least 36 species of Octocorallia (in 13 genera from four families, two orders) were found growing off Carrie Bow Cay, Belize. The distribution and abundance of common species were investigated in the main zones of the transect, the lagoon, patch reefs, and "gorgonian city" in South Water Cut. Observations on natural history, including competition, feeding, and storm damage, are recorded.

## Introduction

This study is the first ever undertaken of the Octocorallia of Carrie Bow Cay. Although the octocorals, in particular those of the taxonomic order Gorgonacea (gorgonians), are a conspicuous and characteristic component of Caribbean coral reefs, work on their ecology and natural history is scarce (Cary, 1914; Kinzie, 1970, 1973; Goldberg, 1973; Opresco, 1973). Since the early monographs of Duchassaing and Michelotti (1860, 1864) only two workers (Deichmann, 1936; Bayer, 1961) have made substantial contributions to the systematics of the group in the western Atlantic. There are, however, several taxonomic lists from various Caribbean locations (Hargitt and Rogers, 1901; Gordon, 1925; Guitart-Manday, 1959; González-Brito, 1970) and one field guide (Cairns, 1977). Only one species, *Plexaura homomalla* (Esper) has received considerable attention from investigators, owing to the commercially important prostaglandins in its tissues (Bayer and Weinheimer, 1974).

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## Material and Methods

Observations were made during 25 SCUBA and 12 snorkel dives, 12–26 April 1979, at habitats near Carrie Bow Cay, including all zones of the transect (Rützler and Macintyre, herein: 9), the lagoon, patch reefs 0.1–2.0 km due southwest, and "gorgonian city," an area 0.6 km north of Carrie Bow Cay having abundant octocorals (Figures 134, 135, 136). At two sites, one on the outer ridge, the other a patch reef, colonies of Octocorallia were labeled with small numbered plastic tags, photographed, identified, and observed during several dives. Photographs were made with a Nikonos camera. Abundance was visually estimated. Identifications were made using field characters combined with standard techniques of sclerite preparations (Bayer, 1961) from branches cut from living colonies. All samples collected are deposited in the Department of Invertebrate Zoology, National History, Smithsonian Institution.

## Species List

(\* = Collected by K. Rützler in 1975, identified by F. M. Bayer; † = collected by R. J. Larson in 1972, identified by R. J. Larson and F. M. Bayer)

### Order ALCYONACEA

#### Family ANTHOTHELIIDAE

*Erythropodium caribaeorum* (Duchassaing and Michelotti)  
*Iciligorgia schrammi* Duchassaing (Figures 134d, 137a)

#### Family BRIAREIDAE

*Briareum asbestinum* (Pallas) (Figure 134a)

## Order GORGONACEA

## Family GORGONIIDAE

*Gorgia mariae* Bayer*G. ventalina* Linnaeus (Figure 135; Plate 3: bottom right, Plate 4: top left, top right, bottom right)*Pseudopterogorgia acerosa* (Pallas) (Figure 135)*P. americana* (Gmelin)*P. bipinnata* (Verrill)\**P. kallos* (Bielschowsky)†*P. rigida* (Bielschowsky)*Pseudopterogorgia* sp. (Figure 134b)*Pterogorgia anceps* (Pallas) (Figure 135)*P. citrina* (Esper)

## Family PLEXAURIDAE

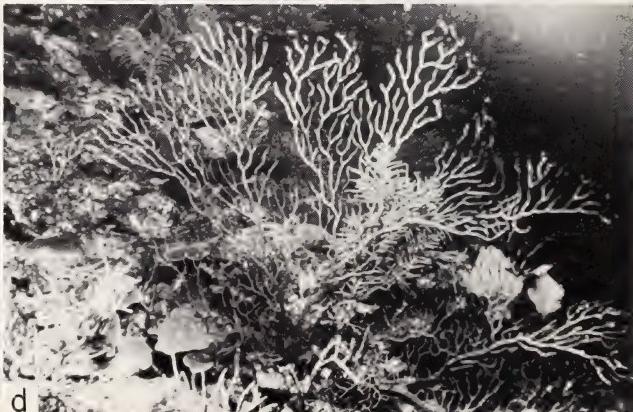
*Eunicea calyculata* (Ellis and Solander)*E. calyculata* forma *coronata* Bayer*E. clavigera* Bayer*E. laciniata* (Pallas)*E. mammosa* Lamouroux (Figure 137b)*E. succinea* (Pallas)*E. succinea* forma *plantaginea* (Lamarck)*Eunicea* spp. (4+)*Muricea atlantica* (Kükenthal)*Muriceopsis flava* (Lamarck)\*†*M. petila* Bayer*Plexaura flexuosa* Lamouroux (Figure 135; Plate 4: bottom right)*P. homomalla* (Esper)*Plexaura* sp.*Plexaurella dichotoma* (Esper)*P. grisea* Kunze\*†*Plexaurella* sp.*Pseudoplexaura flagellosa* (Houttuyn) (Figure 134c)*P. porosa* (Houttuyn)*P. wagenaari* (Stiasny)†*Pseudoplexaura* sp.*Thesea plana* Deichmann

FIGURE 134—Underwater photographs of octocoral species characteristic for some habitats along the barrier reef study transect near Carrie Bow Cay: a, *Briareum asbestinum* (0.4 m tall) lagoon, sand and turtle grass bottom, 4 m deep; b, *Pseudopterogorgia* sp. (1.5 m tall), sand trough habitat, 24m; c, *Pseudoplexaura flagellosa* (over 2 m tall), outer ridge near drop-off, 12 m; d, *Iciligorgia schrammi* (1.5 m tall), fore-reef slope, 20 m.



FIGURE 135—"Gorgonian City" in South Water Cut, 5–10 m deep, characterized by strong currents and a smooth pavement with abundant gorgonians: *Pterogorgia anceps*, lower center; *Plexaura flexuosa*, lower left; *Gorgia ventalina*, upper left; *Pseudopterogorgia acerosa*, upper center (picture width, 3 m).

## Results

**SPECIES DISTRIBUTION AND ABUNDANCE.**—The octocorals of Carrie Bow Cay are represented by at least 36 species in 13 genera, 4 families, and two orders. Traditionally, the Octocorallia have been subdivided into seven orders (Bayer, 1956) but division into fewer orders has at times been accepted (Kükenthal, 1921; Stiasny, 1939). The orders here recognized, distinguished on the basis of skeletal morphology, are Protoalcyonaria, Alcyonacea, Gorgonacea, Helioporacea, and Penicillata. The two orders that occur at Carrie Bow Cay are Alcyonacea and Gorgonacea. The order Alcyonacea now includes the former orders Stolonifera, Telestacea, and Alcyonacea, and the suborder Scleraxonia, all with skeletons composed of sclerites. The order Gorgonacea as now defined

excludes the Scleraxonia and is characterized by octocorals with axial skeletons of "gorgonin," a collagenous protein.

The main factor limiting the distribution of gorgonians and alcyonaceans is the availability of firm substrate; other factors are water movement and light (Kinzie, 1970, 1973). Figures 134 and 135 show octocoral populations and suitable substrates in different habitats. Table 21 lists the distribution of selected octocorals near Carrie Bow Cay by habitat. Figure 136 illustrates the location of taxa within the transect area. The highest number of individuals was observed on the pavement of "gorgonian city," a habitat approximately midway between Carrie Bow and South Water cays. Gorgonian city is characterized by a strong unidirectional tidal current, a smooth, hard substrate, and significant light

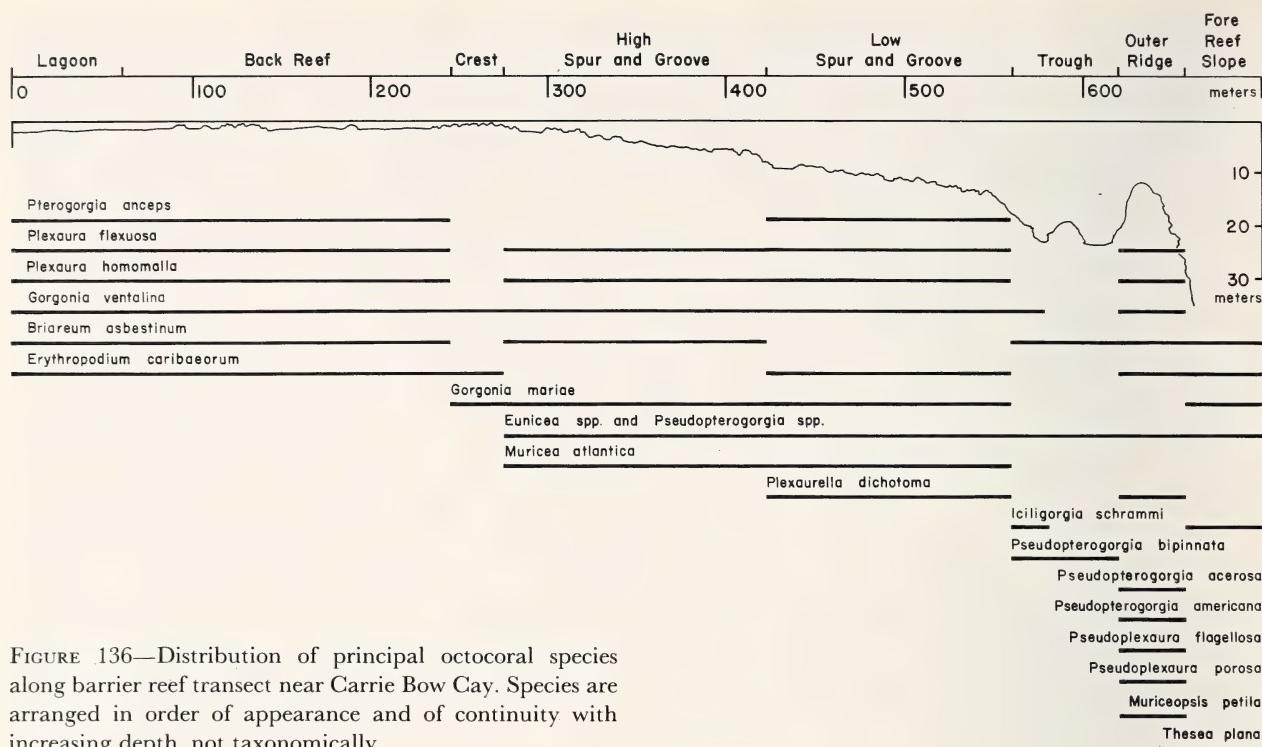


FIGURE 136—Distribution of principal octocoral species along barrier reef transect near Carrie Bow Cay. Species are arranged in order of appearance and of continuity with increasing depth, not taxonomically.

(depth, 5–10 m). Although octocorals are less dense in patch reefs than in gorgonian city, almost the same species occur in both areas. The low-relief spur and groove zone and the outer ridge are next in abundance and have similar species composition. Octocorals in very calm zones (the trough and its slopes and the deep fore-reef slope) are depauperate and largely restricted to species of *Pseudopterogorgia*, *Eunicea*, and *Pseudoplexaura*. Only a few species and a few colonies grow in the calm lagoon, where substrate is a limiting factor. The occurrence of *Erythropodium caribaeorum* at Carrie Bow Cay is conspicuously rare as compared to its common occurrence reported by Kinzie (1973) for Jamaica, who found it often in the rear zone, reef flat, crest, and *Acropora cervicornis* (Lamarck) zones. Although present in the lagoon and crest at Carrie Bow Cay, *E. caribaeorum* is more common in the low-relief spur and groove, outer ridge and, to a depth of 25 m, on the fore-reef slope (Table 21). The only known species in the genus *Erythropodium*, it forms low incrusting rather cryptic colonies so that it is easily overlooked.

**NATURAL HISTORY OBSERVATIONS.**—The flamingo-tongue snail, *Cyphoma gibbosum* Linnaeus, was frequently observed browsing on *Gorgonia ventalina* and occasionally on species of other genera. It has been reported (Birkeland and Gregory, 1975) to prefer gorgoniid octocorals. Fish predation, although observed on California species of *Muricea* (Clarke, 1970) and reported by Randall (1967) from gut contents of a few West Indian species of fishes, was not observed at Carrie Bow Cay. Some colonies of *Gorgonia ventalina* consist of just a main axial skeleton with stubby branchlets, 1–3 cm long. The cause of this unusual shape is unknown and not previously reported but it could be explained by fish or turtle grazing. The axial skeleton appears to be well-covered by living gorgonian tissue. The role that sclerites in the superficial soft tissue play in minimizing predation is unknown. Noxious chemistry may also play an important anti-predator role (Norris and Fenical, herein: 417).

Complete overgrowth by competing *Millepora alcicornis* Linnaeus is fairly common in several

TABLE 21.—Occurrence of selected Octocorallia at various Carrie Bow Cay habitats, confirming presence but not necessarily absence of species from listed habitats; total records of genera *Pseudopterogorgia*, *Eunicea*, and *Pseudoplexaura* indicated as separate categories due to difficulty of field identification to species level; where species identification was possible, records for species in these genera are given also (+ = common; (+) = uncommon)

Species	Transect								Patch reef	Gorgonian city
	Lagoon and back reef	Crest	High spur and groove	Low spur and groove	Inner slope	Trough	Outer slope	Outer ridge		
<i>Erythropodium caribaeorum</i>	(+)	(+)		+				+	+	
<i>Iciligorgia schrammi</i>					(+)				+	
<i>Briareum asbestinum</i>	(+)		+		+	(+)	+	+	+	+
<i>Gorgia mariae</i>		(+)	(+)	(+)					(+)	
<i>G. ventalina</i>	(+)	+	+	+	(+)			+		+
<i>Pseudopterogorgia</i> spp.	(+)	+	+	+	+	(+)	+	+	+	+
<i>P. acerosa</i>								+		+
<i>P. americana</i>								+		+
<i>P. bipinnata</i>						(+)			+	
<i>Pterogorgia anceps</i>	(+)			+					+	+
<i>P. citrina</i>	(+)									+
<i>Eunicea</i> spp.					+	+	+	+	+	+
<i>E. calyculata</i>								+		
<i>E. calyculata</i> f. <i>coronata</i>								+		
<i>E. clavigera</i>								+		
<i>E. laciniosa</i>								+		+
<i>E. mammosa</i>								+		
<i>E. succinea</i> f. <i>plantaginea</i>								+		
<i>Muricea atlantica</i>			+	+						
<i>Muriceopsis petila</i>				+				+	+	+
<i>Plexaura flexuosa</i>	(+)		+	+				+		+
<i>P. homomalla</i>	(+)		+	+				+		+
<i>Plexaurella dichotoma</i>				+				+		+
<i>Pseudoplexaura</i> spp.	(+)		+	+	+	(+)	+	+	+	+
<i>P. flagellosa</i>								+		+
<i>P. porosa</i>								+		+
<i>Thesea plana</i>									+	

species of octocorals, particularly in *Gorgia* and *Pseudopterogorgia*, where the original shape of the colony is commonly maintained by the millepore and is easily recognizable. Overgrowth by sponges is also common. The pinkish *Desmapsamma anchorata* (Carter), is especially noticeable at the southern edge of gorgonian city, where both octocorals and sponges are growing on the rubble and live coral in the sandy zone.

Night dives revealed that octocoral polyps of most genera are expanded at night (presumably

to feed) as well as during the day (Figure 137). *Gorgia ventalina*, however, was not observed expanded at night. It may feed only during the day, or it may rely exclusively on photosynthesis by its zooxanthellae for its energy source. Further observations are needed to determine whether *Gorgia* does expand its polyps at night. The extent of the dependence of octocorals on food capture is unknown; all species reported here except *Iciligorgia schrammi* have abundant zooxanthellae in their tissues. This alcyonacean occurs deeper than

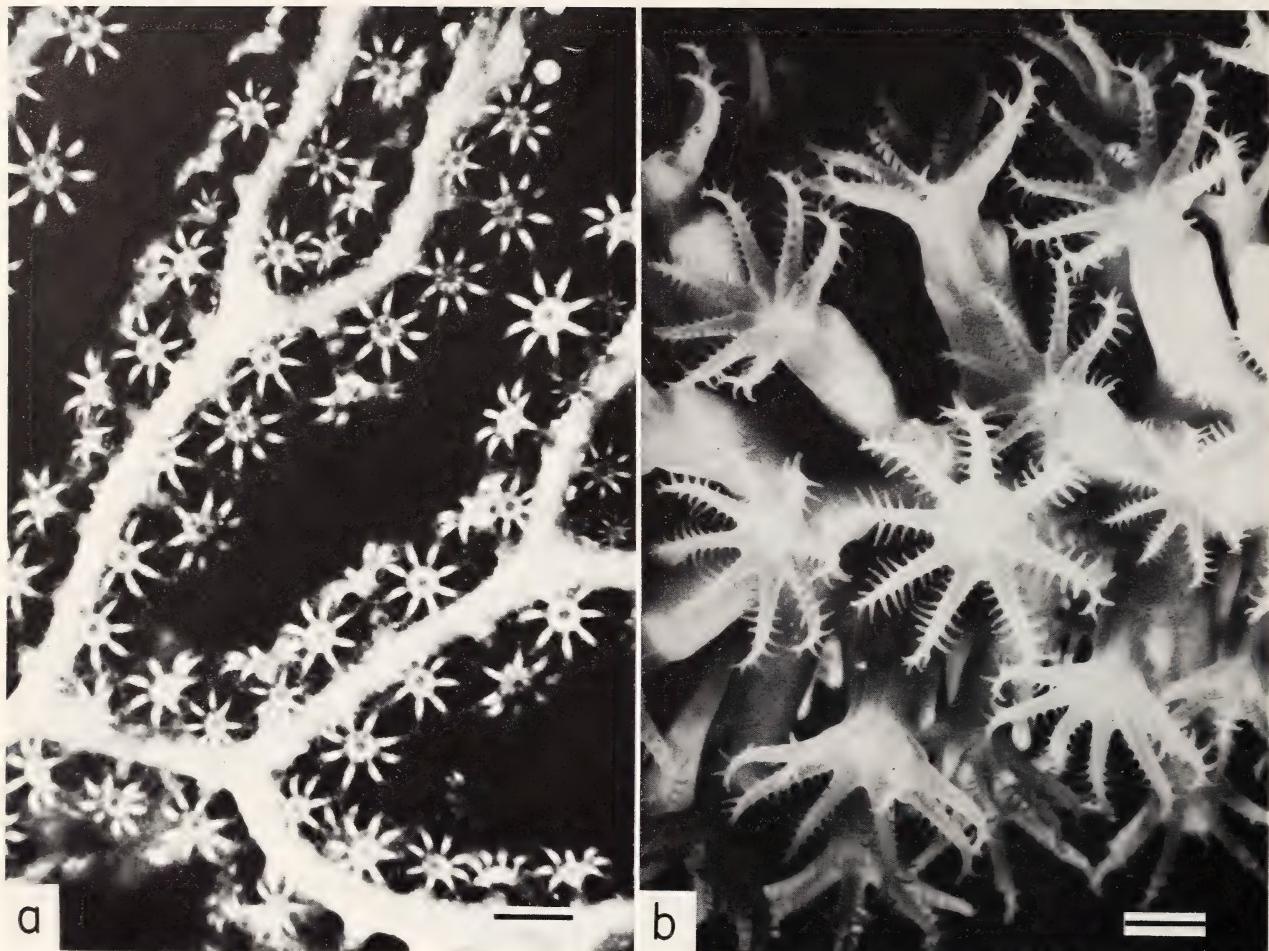


FIGURE 137—Photomacographs of expanded polyps: *a*, *Iciligorgia schrammi*; *b*, *Eunicea mammosa*.  
(Scale: *a* = 5 mm; *b* = 2 mm.)

15–20 m on the fore-reef slope but occasionally also on coral mounds in the trough (20–24 m).

Although long-term studies are necessary to determine growth rates, repair of branches harvested with clippers occurred rapidly. In all 20 colonies (18 species) clipped and revisited at the two sites, the remaining living branch was healing satisfactorily within four days of being cut.

In April 1979, loose and abraded toppled colonies of octocorals lay scattered in the spur and groove zone and in the lagoon. These dying colonies, certainly more common than I have ever observed elsewhere, were apparently dislodged from their substrates during hurricane Greta in September 1978. The extent of the damage can,

of course, only be estimated since there are no pre-storm abundance data. Similar observations, however, were made in Puerto Rico after hurricane Edith (Glynn et al., 1964). Weakening of the substratum around a holdfast by boring organisms has been postulated as the main cause of toppling of the colonies, hence of mortality during storms (Kinzie, 1973).

### Discussion and Conclusions

The Octocorallia of Carrie Bow Cay are abundant and diverse; the species found in this preliminary investigation (at least 36) are comparable both in density and number of species with areas

in the Caribbean known to have abundant gorgonians. Kinzie (1973) lists 43 species in Jamaica, but seven of them live deeper than the typical dives (25 m maximum) of this study. Opresko (1973) reports 29 species from three patch reefs in the Florida Keys. Although most of the species collected at Carrie Bow Cay are known from elsewhere in the Caribbean, at least four appear to be new, for example, species of *Pseudopterogorgia*, *Plexaurella*, and *Eunicea*. The distribution of octocorals is limited by availability of firm substrate as well as by requirements for light and currents. Some species exhibit preference for certain habi-

tats. Four areas, the low-relief spur and groove, the outer ridge, the patch reefs, and gorgonian city are similar in both species composition and abundance. The species of the turbulent crest and high-relief spur and groove zones differ from species of the deep, calm waters of the trough. Some species, such as *Pterogorgia citrina*, abundant only at gorgonian city, exhibit a distribution that is so far unexplained. Colonies of *Erythropodium caribaeorum*, abundant in Jamaica, appear to be less common at Carrie Bow Cay. These and other findings need further investigation for confirmation and explanation.

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# Distribution of Sipuncula in the Coral Reef Community, Carrie Bow Cay, Belize

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and Ian G. Macintyre

## ABSTRACT

A survey of sipunculan fauna associated with coral rock and rubble along a transect across the coral reef at Carrie Bow Cay, Belize, revealed eight species, six of which inhabited burrows within rock samples and two of which occurred in crevices and crannies. Comprising 95 percent of the collection, the four most abundant species were, in order of abundance: *Lithacrosiphon alticus* Ten Broeke; *Aspidosiphon brocki* Augener; *Phascolosoma perlucens* Baird; and *Paraspidosiphon steenstrupi* (Diesing). The greatest concentration of sipunculans, measured as number per square meter of surface area of rock, occurred in reef-crest material. Sipunculans were least abundant in material from the patch-reef zone of the back reef and from the fore-reef slope. The four most abundant species showed a distinct distributional pattern along the transect. Generally, sipunculans from the same reef habitat were densest in fresh, relatively unaltered coral rock having little secondary infill of calcite cement and a rather uniform skeletal framework characteristic of species of *Porites* and *Acropora*. Samples of more highly eroded, commonly well-cemented, and presumably older rocks contained few, if any sipunculans. Aspects of sipunculan distribution suggested for further study include reproductive strategy and variations in substrate characteristics.

## Introduction

Marine worms of the phylum Sipuncula are common inhabitants of coral reef communities

throughout the world. They occupy a variety of habitats within the community: sand burrowing species occur in sand flats of lagoons and in sediments surrounding the bases of coral growths; other species inhabit crevices in rubble or live within algal mats on surfaces of coral boulders; still others dwell in burrows that they excavate in coral rubble and in coral-rock framework. These rock-boring species, often occurring in great densities, contribute to the erosion of reefs by weakening the supporting structures of the corals and thus increasing their susceptibility to breakage and destruction by physical stresses related to currents and wave action. Numerous papers have referred to the boring activities of sipunculans in coral limestone and to their possible role in reef destruction (Gardiner, 1903; Otter, 1937; Rice, 1969, 1975a, 1976; Rice and Macintyre, 1972).

This study is a preliminary survey of the sipunculan fauna associated with the reef at Carrie Bow Cay, Belize. From the distributions of sipunculans in different zones of this coral reef community and in different types of coral rock, habitat preferences of the rock-boring species are suggested. Reproductive patterns that may have a bearing on distribution are also noted.

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## Materials and Methods

Observations and collections were made during three 10-day trips to Carrie Bow Cay in 1972,

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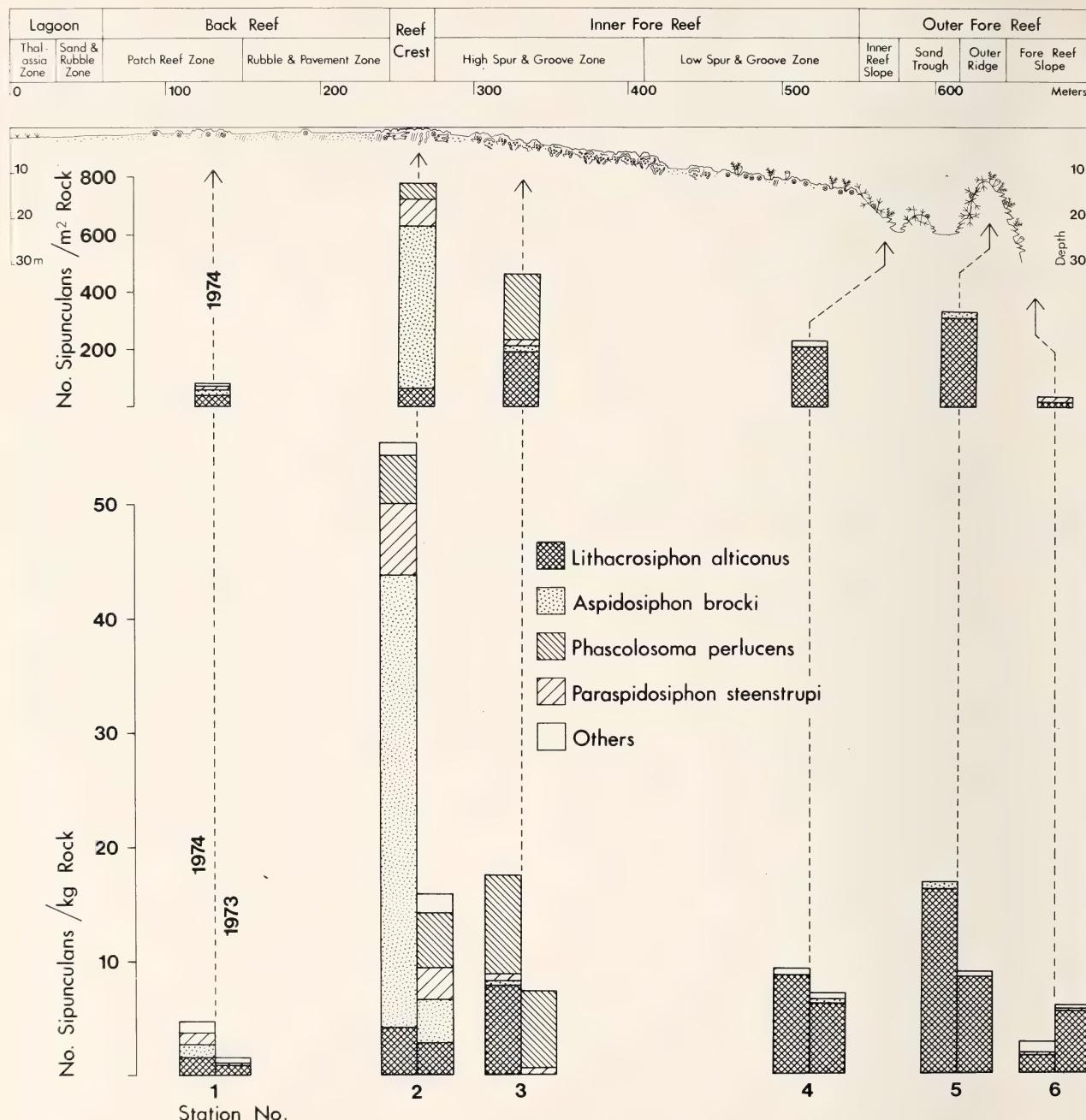


FIGURE 138.—Density of sipunculans in coral rock along the transect of the reef, Carrie Bow Cay, 1973, 1974. Density is expressed as numbers of sipunculans per kilogram of rock (1973, 1974) and as numbers of sipunculans per square meter of rock surface (1974), for each of six stations.

1973, and 1974. Species of sipunculans on the reef were surveyed in 1972, and types of coral rock inhabited as well as numbers of sipunculans per kilogram of rock were determined in 1973. These observations were repeated in 1974 and, in addition, numbers of sipunculans per unit of surface area of rock were determined.

**COLLECTING SITES.**—Sipunculans were collected at numerous sites along a transect across different zones of the reef to the north of Carrie Bow Cay (Figure 138). The transect extends from the *Thalassia* beds of the lagoon across the back reef, reef crest, inner fore reef and outer fore reef to a depth of 35 m on the fore-reef slope. This transect, which has been the site of many other studies, is described in detail by Rützler and Macintyre (herein: 9). Density of sipunculan species was examined at six stations ranging in depth from intertidal waters at the reef crest to 35 m on the fore-reef slope (Figure 138).

**COLLECTION OF ROCK.**—On average, four rocks were collected at each station but this number varied from two to 10, depending on their availability and size; the greatest number was collected at station 6 on the outer fore-reef slope. These were usually free boulders of coral rock found on the surface of the sediment. Samples of limited size (0.4 to 4.6 kg, averaging 1 to 2 kg) were selected at random at each site.

**DESCRIPTION OF ROCK SAMPLES.**—Length, width, thickness, and general shape of each rock were recorded along with associated flora and fauna. Rocks were weighed to the nearest gram, and surface area was calculated by covering the rocks with aluminum foil and converting the weight of the foil to square meters, after the method of Marsh (1970).

**EXTRACTION OF SIPUNCULANS.**—Except for small fragments saved for petrographic analysis, each rock was completely fractured with a rock pick and chisel and all sipunculans were extracted. Species were identified, counted and, in most cases, preserved in 70 percent ethyl alcohol. A few specimens were kept alive for laboratory observations on spawning and developmental patterns.

**IDENTIFICATION OF CORAL ROCK.**—Component coral species of each rock fragment were identified. Other factors examined included the character and distribution of encrusting biota, the destruction of coral skeleton by bioerosion, and secondary infilling by submarine lithification. The extent of secondary infilling by magnesium calcite cement is said to be directly related to both the length of time and degree of water agitation to which the substrata have been exposed (Macintyre, 1977). Borings of known species were saved for a separate study on boring mechanisms of rock-dwelling sipunculans (Rice, 1976).

## Results

**AEREAL DISTRIBUTION.**—Of the eight species of sipunculans collected from coral rock and rubble at Carrie Bow Cay (Table 22), six species were found in burrows within the rocks and two in crevices or crannies. The four most abundant species, which comprised 95 percent of the specimens collected over the three-year period, were rock-boring species. In order of abundance, they were: *Lithacrosiphon alticonus* Ten Broeke, *Aspidosiphon brocki* Augener, *Phascolosoma perlucens* Baird, and *Paraspidosiphon steenstrupi* (Diesing).

The most common species (47 percent of specimens collected) was *Lithacrosiphon alticonus*, which is also referred to in the literature by its synonym, *L. gurjanovae*. It was found at all depths along the transect, including intertidal sites, but was most common in depths of 3 to 35 m. This small species, which averages about 10 mm in retracted length, possesses an anterior calcareous cone, typical of the genus, that functions to close the opening of the boring when the anterior retractable portion of the body—the introvert—is withdrawn (Figure 139a). Endemic to the Caribbean, *L. alticonus* has been reported from beachrock, recent unaltered coral rock, and highly eroded coral rock (Ten Broeke, 1925; Murina, 1967; Rice, 1975a).

Twenty-three percent of the specimens were *Aspidosiphon brocki*, found in small numbers at

TABLE 22.—Sipunculans collected from coral rock at Carrie Bow Cay, 1972, 1973, 1974

Sipunculan species	Number collected (3-year total)	Percent of total sample	Habitats
<i>Aspidosiphon brocki</i>	261	23.0	Borings in recent coral limestone; commonly intertidal to 1 m depth; rubble of <i>Porites porites</i> , <i>P. astreoides</i> , <i>Acropora palmata</i>
<i>Golfingia sp.</i>	6	0.5	Crevices and holes of coral rock; scattered throughout coral reef community
<i>Lithacrosiphon alticonus</i>	531	47.0	Borings in all types of coral rock from fresh, dense coral to extensively bored and eroded limestone; most common in deeper water, 3–35 m
<i>Paraspidosiphon fischeri</i>	9	0.8	Borings in all types of coral rock; most common in rubble of <i>Porites porites</i> in shallow water
<i>P. speciosus</i>	8	0.7	Borings usually in eroded coral rock, with secondary infill; most frequent in deeper waters of outer reef slope
<i>P. steenstrupi</i>	107	9.4	Borings in all types of coral rock throughout reef; at all depths, most common at reef crest; <i>Porites astreoides</i> , <i>Acropora palmata</i>
<i>Phascolosoma perlucens</i>	171	15.1	Borings in recent coral limestone; shallow waters, intertidal to 3 m; abundant in rocks of <i>Acropora palmata</i> and <i>Agaricia</i> sp.
<i>P. varians</i>	40	3.5	Crevices and holes of coral rock; algal mats covering rocks; most abundant in intertidal and shallow waters

various depths along the transect and in great densities at the reef crest. The smallest species collected, it ranges from 3 to 10 mm in length of the trunk. The thickened anterior and posterior shields of the trunk are characteristic of the genus (Figure 139b), although the posterior shield may be weakly developed in specimens that are regenerating after undergoing asexual reproduction. Unlike species that reproduce sexually, *A. brocki* reproduces asexually (Figure 139c) by constricting the posterior end to form a juvenile individual; thereafter, the posterior end of the adult regenerates (Rice, 1970). This species was first described from the Philippines and has been reported since from calcareous rock throughout the Caribbean (Murina, 1967; Rice, 1970, 1975a).

*Phascolosoma perlucens*, which comprised 15 percent of the sipunculans collected, was found only in shallow waters of the reef crest and the high-relief spur and groove zone. Averaging 30 to 40 mm in extended length, this long, slender species has concentrations of conical papillae at the pos-

terior end and at the base of the introvert. The introvert is marked dorsally by bands of reddish-brown pigment (Figure 139d). Frequently referred to in the literature by its junior synonym, *Phascolosoma dentigerum*, this circumtropical species has been reported as the most common rock-boring species in the Caribbean (Rice, 1975a).

*Paraspidosiphon steenstrupi* made up only 9 percent of the collection. Although found in small numbers, it occurred along most of the transect. This species, which has characteristic anterior and posterior shields, averages 20 mm in length when the introvert is retracted (Figure 139e). Circumtropical in distribution, it is especially common throughout the Indo-Pacific and is reported from a number of localities in the Caribbean (Shipley, 1903; Fischer, 1922a, 1922b; Ten Broeke, 1925; Murina, 1967; Rice, 1975a).

The size and shape of the borings of sipunculans in coral rock reflect the size, shape, and activity of the inhabiting species (Rice, 1969, 1975a). Borings of *Lithacrosiphon alticonus*, a rela-

tively inactive species, are generally straight and cylindrical, and the closed end of the passage is distinctly rounded. The small species, *Aspidosiphon brocki*, has a short, narrow boring, usually straight and always near the surface, extending at any angle from the surface into the rock. The borings of *Phascolosoma perlucens*, a larger, more active species capable of considerable extension and contraction, are long and winding, sometimes extending deep into the interior of the rock. The unpredictable course of these borings makes it difficult to extract specimens without injury. The borings of *Paraspidosiphon steenstrupi* are also long and penetrate far into the rock, but they are usually less sinuous than those of *P. perlucens*.

**DISTRIBUTION ALONG THE TRANSECT.**—Available surface area of substrate rock is an important limiting factor for sipunculan habitation; among rocks of different thickness, shape, and size, a

comparison of densities of the indwelling sipunculan fauna is most meaningful when numbers of sipunculans are related to surface area. In the 1974 data considered below, densities of species at the six transect stations are calculated as numbers per square meter of rock surface (Figure 138).

The greatest concentration of sipunculans was found on the reef crest (station 2). The substratum of this zone, partially exposed at low tide and subject to strong wave action, consists of in-place scattered live coral heads on a coral rock pavement, coral boulders, and coral rubble. The coral rock, predominantly *Porites astreoides* Lamarck and *Acropora palmata* (Lamarck), contains traces of sub-microscopic magnesium calcite (Macintyre, 1977) and consists of a relatively unaltered aragonite coral skeleton. All four rocks (totaling 4 kg) from this station consisted of dead *Porites astreoides*. Growths of coralline and filamentous

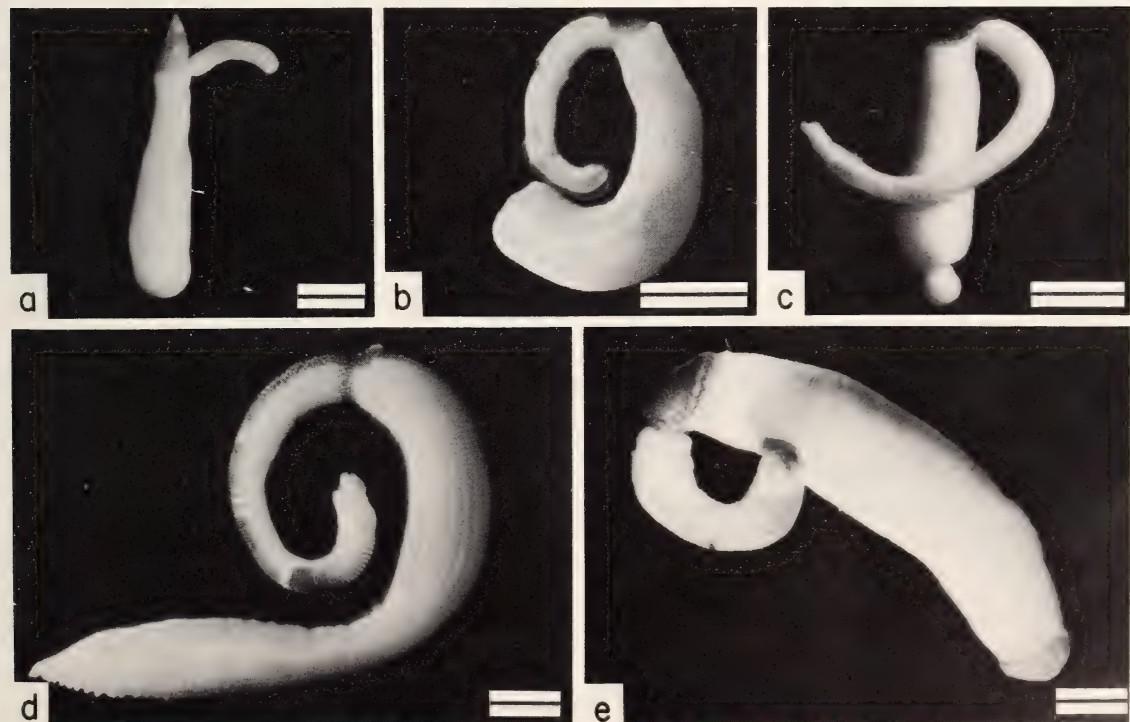


FIGURE 139.—Common sipunculans from Carrie Bow Cay: *a*, *Lithacrosiphon alticonus*; *b*, *c*, *Aspidosiphon brocki* (specimen in *c* undergoing asexual reproduction, division will occur at the point of the constriction, the posterior portion forming a juvenile individual); *d*, *Phascolosoma perlucens*; *e*, *Paraspidosiphon steenstrupi*. (Scale = 2 mm.)

algae, some encrusting sponges and foraminifers (*Homotrema* sp.) were scattered on the rock surfaces. Other than sipunculans, the few living organisms within the rocks consisted of a few polychaetes and boring barnacles (*Lithotrypa* sp.), and some vermetids and boring sponges near the surface.

All four common rock-boring sipunculan species at Carrie Bow Cay occurred at the reef crest; the dominant species, here accounting for 71 percent of the individuals, was *Aspidosiphon brocki*. The order of abundance of the other three species was *Paraspidosiphon steenstrupi*, and equal numbers of *Lithacrosiphon alticonus* and *Phascolosoma perlucens*. Other species associated with the rocks, either in old cavities or in crevices but showing no evidence of forming their own burrows, were *Phascolosoma varians* and an unidentified species of *Golfingia*.

The second largest concentration of sipunculans was found in depths of 2 to 3 m in an area of large coral buttresses seaward of the reef crest (station 3). Known as the high-relief spur and groove zone, it is dominated by a substratum of living corals, coral rubble, and boulders interspersed with sand patches and loose coral that cover a smooth rock pavement. Whereas the reef crest is in part intertidal, the high-relief spur and groove zone is entirely subtidal. Of the four rocks examined (totaling 5.6 kg), one was fresh *Porites astreoides* with no infill. It was difficult to break and contained only one sipunculan. Two rocks were fresh *Acropora palmata* and the fourth fresh *Agaricia* sp. One had a trace of submicrosucrosic magnesium calcite infill.

The most abundant species at this station were *Phascolosoma perlucens* and *Lithacrosiphon alticonus*. Only small numbers of *Phascolosoma varians*, *Paraspidosiphon steenstrupi*, and *Aspidosiphon brocki* were present.

Next in abundance of sipunculans was station 5 on the outer ridge in 15 m of water, where the bottom is primarily living coral with patches of sand and coral rubble. Two rocks totaling more than 5 kg from this area consisted of fresh *Porites astreoides* having little or no infill. One contained numerous *Lithacrosiphon alticonus* and a few *Aspi-*

*dosiphon brocki*; its upper surface was covered with red boring sponges and encrusting and filamentous algae, whereas the lower surface was almost barren, with a lesser amount of crustose coralline algae and red sponges. This second rock contained only a few polychaetes and one specimen of *L. alticonus*; around its edges were several patches of live coral, also encrusting bryozoans, crustose coralline algae, and a white sponge. Its internal composition was similar to that of the first rock, except that one surface contained more submicrosucrosic magnesium calcite infill.

Next in abundance of sipunculans was station 4 located in 23 m of water at the base of the inner reef slope; here the substratum is mainly sandy sediment with small amounts of scattered rubble and a few heads of live *Montastrea annularis* (Ellis and Solander), dominated by flattened growth forms. Of the three rock samples (6.7 kg) collected, two were *M. annularis* and one *Manicina areolata* (L.). One *Montastrea annularis* rock had considerable crustose coralline algal cover and extensive borings at the surface and contained numerous sipunculans of the genus *Lithacrosiphon*. The other *M. annularis* rock had very little covering growth and was nearly devoid of sipunculans. The third rock had an open porous meandroid skeleton and large masses of boring sponges near the surface. It contained many sipunculans, mainly *Lithacrosiphon*, but they were less concentrated than in the first rock. The sipunculan burrows commonly ran parallel to the dissepiments of the coral skeleton.

The remaining two stations at either end of the transect had the fewest sipunculans. Station 1 in the patch-reef zone of the back reef (depth about 1 m) had substrata of scattered rubble and boulders in a sand matrix between live coral patches (dominantly *Montastrea annularis*). The four rocks from this station were composed of *M. annularis* (total weight, 3.5 kg). Surfaces adjacent to the sand were almost bare, with scattered foraminifers (*Homotrema* sp.) and some crustose coralline algae. On the upper surfaces, crustose coralline algae and red and brown filamentous algae were common. The degree of infiltration and erosion

and the amount of freshly preserved coral skeleton varied from a highly eroded skeleton with extensive sediment-rich submicrosucrosic magnesium calcite to an almost freshly preserved skeleton. The highest density of sipunculans was found in the rock having the most intact skeleton and the least calcite infill. Species of sipunculans at station 1 were *Lithacrosiphon alticonus*, *Aspidosiphon brocki*, *Paraspidosiphon steenstrupi*, and *Phascolosoma varians*.

Station 6 was located on the fore-reef slope in depths of 25 to 35 m. The substratum exposed between the rich cover of octocorals and dominantly platy coral colonies was in-place coral framework with a thin cover of *Halimeda*-rich sand and scattered rubble. The coral rock from this zone was highly eroded and infiltrated with sponge growth. The 10 rocks collected (total weight, 14 kg) were covered with numerous sponges, some compound tunicates, tunicates, coralline algae, "leafy" brown and green algae, bryozoans, and small serpulid worm tubes. These rocks were lying on, or were partially embedded in the sediment. Three were so extensively bored, infilled, and lithified with dense microcrystalline and porous submicrosucrosic magnesium calcite that the coral skeleton could not be recognized. Five corals were identified in the other seven rocks: *Porites astreoides*, *Meandrina* sp., *Stephanocoenia* sp., *Agaricia* sp., and *Siderastrea siderea* (Ellis and Solander). Two rocks were fresh coral with their skeletal structure intact and with little secondary infill. The others were water worn and extensively bored and they contained some submarine lithification. Boring sponges had infiltrated the rocks. Empty borings and other large holes within the rocks were filled with sand and mud and patches of submicrosucrosic magnesium calcite. Few sipunculans were found in any of these rocks, the most occurring in a sample of fresh *Porites astreoides* that contained five *Lithacrosiphon alticonus* and one *Paraspidosiphon steenstrupi*. *Paraspidosiphon speciosus* was found only in highly eroded samples. A few polychaetes, alphaeid shrimp, and an echiuran occurred within the sand-filled holes in the rock.

When density of sipunculans was measured as

number per kilogram of rock, the distribution of species and relative densities were almost the same as when measured as number per square meter of surface area. Data from 1973 and 1974 are compared in Figure 138.

**DISTRIBUTION IN DIFFERING ROCK TYPES.**—Of the nine types of coral rock in the 1974 collections, *Porites*, *Agaricia*, and *Acropora* specimens contained the greatest density (Table 23) and diversity of sipunculans. These rocks were not distributed equally along the transect; only *Porites astreoides* and *Agaricia* sp. were collected at more than one station. *Porites* rock, the most common, was found at four stations: reef crest, high-relief spur and groove, outer ridge, and fore-reef slope. *Porites* rock at the reef crest contained, in order of abundance, *Aspidosiphon brocki*, *Paraspidosiphon steenstrupi*, and equal numbers of *Lithacrosiphon alticonus* and *Phascolosoma perlucens*. The sipunculan fauna in *Porites* rocks from other stations consisted almost entirely of *Lithacrosiphon alticonus* (Figure 140). All *Porites* samples were recent, unaltered coral rock having little secondary calcite infill. The density of sipunculans varied considerably, even among rocks of the same composition at the same locality (Figure 140).

**OBSERVATIONS ON REPRODUCTIVE ACTIVITY.**—After removal from coral rock, specimens of *Phascolosoma perlucens*, *Phascolosoma varians*, *Paraspidosiphon steenstrupi*, and *Lithacrosiphon alticonus* were

TABLE 23.—Density of sipunculans in different types of coral rocks

Coral species	Rocks		Sipunculans	
	Number	Weight (kg)	Total number	Number/kg rock
<i>Acropora palmata</i>	4	10.78	75	6.96
<i>Agaricia</i> sp.	2	3.34	27	8.08
<i>Manicina</i> sp.	—	—	—	—
<i>Meandrina</i> sp.	—	—	—	—
<i>Montastrea annularis</i>	7	8.09	50	6.18
<i>Porites astreoides</i>	6	11.10	72	6.49
<i>Porites</i> sp.	4	5.37	22	4.10
<i>Siderastrea siderea</i>	7	10.84	61	5.63
<i>Stephanocoenia</i> sp.	—	—	—	—

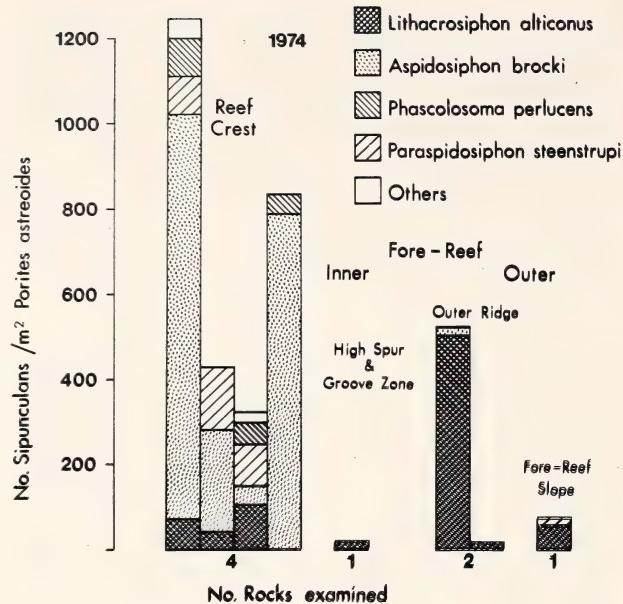


FIGURE 140.—Density of sipunculans along the transect in *Porites astreoides* rock, Carrie Bow Cay, 1974.

kept alive in the laboratory for one to two months for observations on spawning. The first two species were observed to spawn in April and *Paraspidosiphon steenstrupi* in June. *Lithacrosiphon alticus* did not spawn even though oocytes in the body cavity were visible through the body wall of many specimens. A planktotrophic larval stage occurs in the development of *Phascolosoma perlucens* and *P. varians*. Although development of *Paraspidosiphon steenstrupi* has not been observed, the small size of the egg and the relatively sparse yolk indicate that development of this species is also planktotrophic.

Specimens of *Aspidosiphon brocki*, known to reproduce asexually by constricting the posterior end to form a new individual (Rice, 1970), were examined for evidence of reproductive activity. Nineteen percent of the April 1974 collections had posterior constrictions. An additional eight percent had juveniles in their burrows.

### Discussion and Conclusions

The rock-boring sipunculans at Carrie Bow Cay showed specific distribution within the reef

community, the greatest diversity occurring at the reef crest where six species (of which four were common rock borers) were found. The four rock borers, found together only in the reef crest and high-relief spur and groove zones, each had distinctive distribution on the transect. *Lithacrosiphon alticus* was found all along the transect in both deep and shallow waters but it was most abundant from the high-relief spur and groove zone to the outer ridge. *Aspidosiphon brocki* was dominant at the reef crest but occurred only sporadically and in small numbers in other areas. *Paraspidosiphon steenstrupi* was most abundant at the reef crest but occurred in small numbers along most of the transect. *Phascolosoma perlucens* was limited to the reef crest and to the shallow waters of the fore-reef zone. In being related to reef zonation, the overall distribution of these four sipunculan species must also be related directly or indirectly to physical parameters that control this zonation, the most important of which are water agitation and light intensity, both depth-dependent factors.

The substratum most densely inhabited by sipunculans was generally fresh coral rock with almost uniform skeletal framework, as is characteristic of *Porites* and *Acropora* species, and with relatively little secondary calcite cement infill. The more highly eroded, water-worn, older rocks on the transect generally contained few, if any, sipunculans. Internally, such rocks showed considerable infilling of calcite cement and were heavily infiltrated by boring sponges. The presence of numerous tunnels and cavities suggested previous habitation by boring organisms such as sipunculans. The absence of extant sipunculans might be explained by natural death of specimens that had formed the borings, by natural succession of boring organisms, or by death due to a catastrophic event (for example, rocks having been buried in sediment). The lack of new boring by sipunculans might be due to unavailability of sufficient solid substratum in rocks that are heavily bored and infiltrated with sponges.

Typically, the rocks containing sipunculans were covered by sponges and algal growths (filamentous, leafy and crustose coralline). Encrusting organisms such as bryozoans and the foraminini-

feran *Homotrema* sp. occurred most commonly but not exclusively on the underside of the rock samples. Sponges, along with a host of other invertebrates such as crabs, stomatopods, alpheid shrimp, isopods, barnacles, certain polychaetes, and bivalves, were found within the rocks—either in interstices and cavities or in burrows that they had formed in the rocks. Organisms in burrows included the boring sponges, polychaetes of the families Spionidae, Sabellidae, and Serpulidae as well as certain boring bivalves (*Lithophaga* sp. and *Gastrochaena* sp.) and boring barnacles (*Lithotrya* sp.). Sipunculans were rarely found in rocks with barren surfaces and were not observed in live portions of coral colonies. Sipunculan borings open most commonly on the upper surfaces and sides of rocks, but also on the lower surface lying on the sand. Boring sipunculans are known to feed on the surfaces of rocks they inhabit, ingesting bits of debris and sand entrapped in the surface cover and possibly pieces of algae (Rice, 1969, 1975a); thus the epibionts are probably important to the survival of the animals within the rock, although details of this association remain to be investigated.

The present study points out pertinent factors for future evaluation of the relative influence of various physical and biotic factors on distribution of rock-dwelling sipunculans in the coral community. The greater density of animals in recent unaltered coral rock from Carrie Bow Cay than in highly eroded rock indicates the probable importance of internal structure of the rock to infiltration by boring sipunculans. On the other hand, the observation that different species may inhabit the same type of coral rock in different areas of the reef community suggests that physical factors associated with locality—such as agitation and depth of water—may be even more significant than coral skeleton in determining specific distribution. These data, however, must be considered preliminary because the same rock types could not be collected in each reef locality. Moreover, the variation in density of sipunculans in similar rocks from the same locality indicates the complexity of the problem and the necessity for more rigidly controlled quantitative procedures. Fur-

ther studies should compare the relative significance to rock-boring sipunculans of the type of coral skeleton and degree of secondary infilling. Tests of habitat preference could be made by transplanting rocks of known composition to different parts of the reef community and by examining these rocks over a period of years.

Many other questions concerning colonization of coral rock by boring sipunculans remain to be explored. Factors affecting larval settlement are unknown, yet they undoubtedly play an important role in determining distribution of those species having planktotrophic larvae, such as *Phascolosoma perlucens* (Rice, 1975b). Distribution of species lacking planktotrophic larvae would be regulated by different factors. For example, an explanation for the localized concentrations of *Aspidosiphon brocki* might be found in the pattern of asexual reproduction of this species. Young, crawling juveniles, unable to traverse great distances, probably would colonize either the same rock as the parent or other rocks in the vicinity.

Recent studies on infaunal communities of coral rock have suggested that surface area, porosity of rock, percentage of live coral and epibionts may influence infaunal distribution and colonization (Hutchings, 1978). Therefore, reliable quantitative data and improved methods of approach are obviously necessary. Brock and Brock (1977) proposed the use of acid dissolution of rock for quantitative removal of specimens previously preserved in formalin. Hutchings (1977) measured exposed surface area of substrata by coating surfaces with Playtex rubber which, after drying, can be peeled off, traced and measured with a polar planimeter. Various other techniques for measurements and sampling have been listed in a recent review of research methods for studies of coral reef cryptozoa (Hutchings, 1978). To date, most research efforts on specific groups of rock-dwelling fauna in coral reefs have focused on polychaetes, although sipunculans have been recognized as a significant component of the coral-rock infauna (Kohn and Lloyd, 1973; Peyrot-Clausade, 1974; Hutchings, 1974, 1977). It is hoped that future studies will apply the more refined current techniques to the rock-boring si-

punculans and thus may provide a better understanding of their distribution in the reef commu-

nity and of their significance to the total reef ecosystem.

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# Anthuridea (Crustacea: Isopoda) of Carrie Bow Cay, Belize

Brian Kensley

## ABSTRACT

Fourteen species of anthurid and paranthurid isopods from Carrie Bow Cay, Belize, are considered. These include two new genera, *Belizanthura* and *Minyanthura*, and seven new species, *Apanthura geminsula*, *Belizanthura imswe*, *Mesanthura fasciata*, *M. punctillata*, *M. reticulata*, *Minyanthura corallicola*, and *Paranthura caribbiensis*. These species are relatively abundant in shallow water (1.5 m or less) habitats such as coral rubble and coarse sandy sediments, but scant in deeper (6–24 m) sediments. Few species were observed in the entire range from the intertidal zone to depths of 40 m. Male anthurids found in the plankton show morphological adaptations suggesting that they had left their substrates for reproductive rather than feeding purposes.

## Introduction

During January–February 1978 the author carried out two weeks of collecting at Carrie Bow Cay, Belize, from a variety of habitats, ranging from very shallow water to depths of about 40 m. Seventeen species of anthurids and paranthurids were collected (three represented by single specimens, and not treated in this paper). This is the highest number of anthuridean species taken in any single locality, and probably indicates that many species await discovery upon more careful investigation of different substrate and habitat types. This high number of species, and in some

cases, high numbers of specimens, is a strong indication of the important role the group often plays in shallow-water ecosystems. Very little is known of the biology, especially the feeding of these animals. It is hoped that future living specimen studies in the laboratory will provide such data.

Material is deposited in the National Museum of Natural History, Smithsonian Institution. In the accompanying figures a scale (in millimeters) is given only for the entire animal in dorsal view.

**ACKNOWLEDGMENTS.**—My thanks are due the following Smithsonian personnel: R. J. Larson for information and for specimens from horizontal plankton sampling, C. A. Child for help in collecting and sorting, J. N. Norris for algal identifications, A. C. Cohen for material collected, and F. D. Ferrari for making earlier Belize material available. I am very grateful to T. E. Bowman for reading the manuscript and for his many useful comments and criticisms.

## Species List

### Suborder ANTHRIDEA

#### Family ANTHRIDAE

##### *Apanthura* Stebbing

*Apanthura geminsula*, new species

*Apanthura signata* Menzies and Glynn

##### *Apanthuroides* Menzies and Glynn

*Apanthuroides millae* Menzies and Glynn

##### *Belizanthura*, new genus

*Belizanthura imswe*, new species

##### *Mesanthura* Barnard

*Mesanthura fasciata*, new species

*Mesanthura paucidens* Menzies and Glynn

*Mesanthura pulchra* Barnard

*Mesanthura punctillata*, new species

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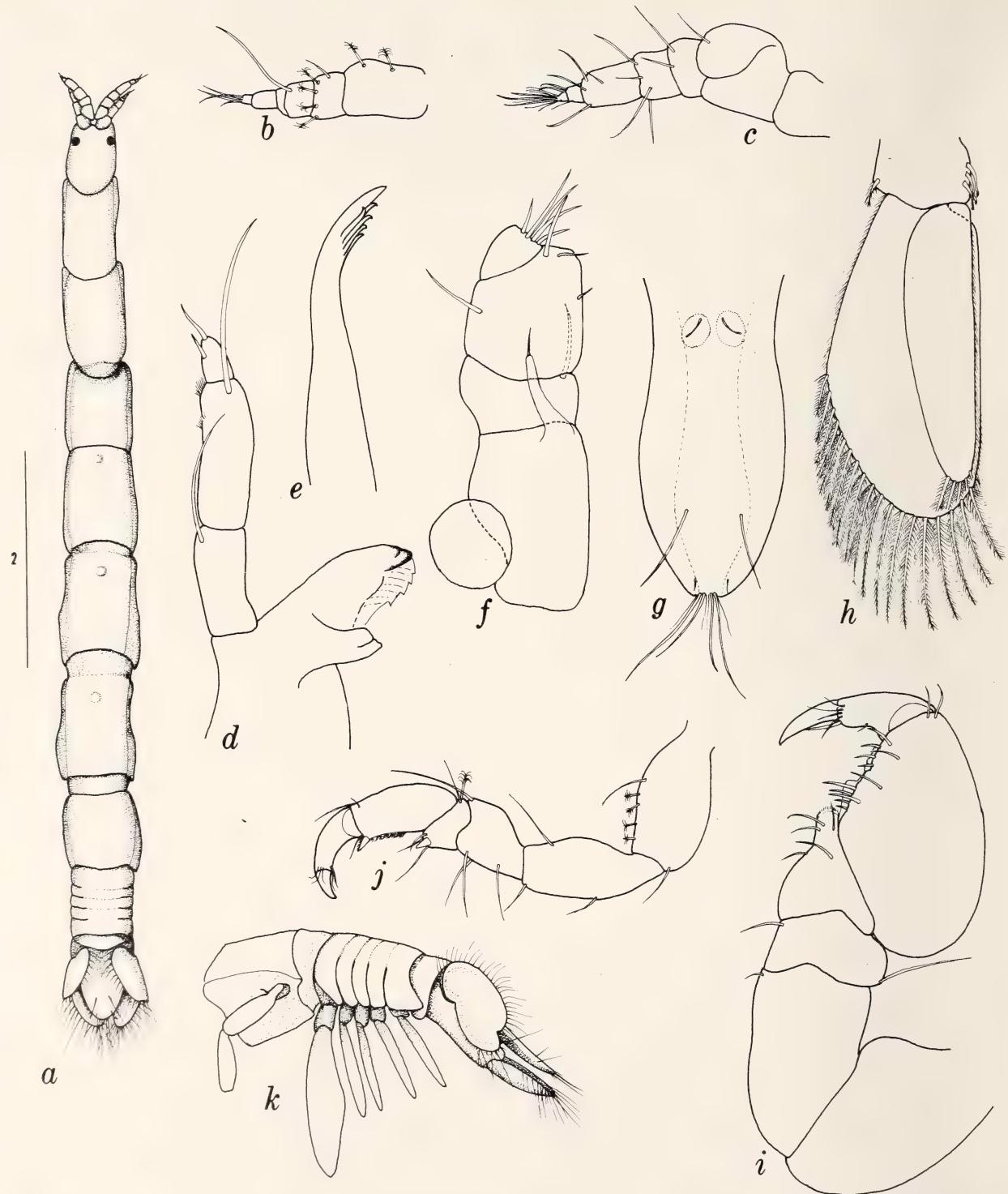


FIGURE 141.—*Apanthura geminsula*, new species, holotype, ♀: *a*, complete specimen; *b*, antennule; *c*, antenna; *d*, mandible; *e*, maxilla; *f*, maxilliped; *g*, telson; *h*, pleopod 1; *i*, pereopod 1; *j*, pereopod 7; *k*, pleon in lateral view.

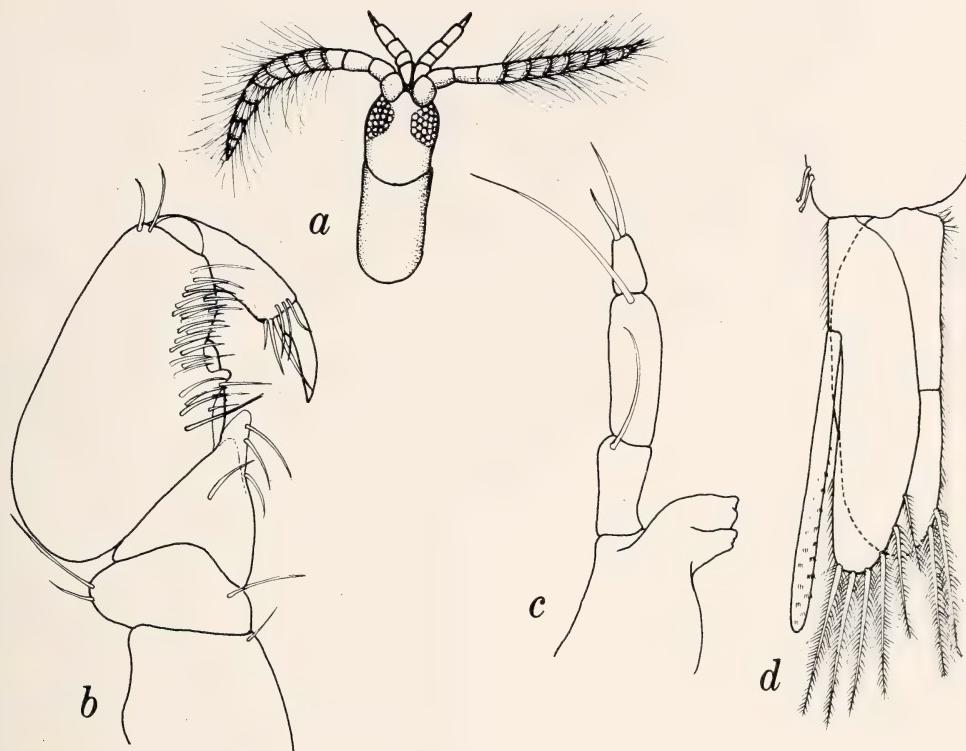


FIGURE 142.—*Apanthura geminsula*, new species, ♂: *a*, cephalon; *b*, pereopod 1; *c*, mandible; *d*, pleopod 2.

*Mesanthura reticulata*, new species

*Minyanthura*, new genus

*Minyanthura corallicola*, new species

*Pendanthura* Menzies and Glynn

*Pendanthura tanaiformis* Menzies and Glynn

Family PARANTHURIDAE

*Accalathura* Barnard

*Accalathura crenulata* (Richardson)

*Paranthura* Bate and Westwood

*Paranthura caribbiensis*, new species

*Paranthura infundibulata* Richardson

#### Suborder ANTHRIDEA

##### Family ANTHRIDAE

##### *Apanthura*, Stebbing

##### *Apanthura geminsula*, new species

FIGURES 141, 142

DESCRIPTION OF FEMALE.—Body moderately indurate, semitranslucent when alive, lacking any

pigmentation. Cephalon with low triangular rostrum, not extending beyond anterolateral corners. Eyes dorsolateral. Body proportions:  $C < 1 = 2 > 3 < 4 = 5 = 6 > 7$ . Pereonites 4, 5, and 6 each with middorsal shallow pit. Pleonites 1–5 fused, but indicated ventrolaterally, with shallow dorsal grooves indicating lines of fusion; pleonite 6 free. Telson thin, hardly indurate, with hyaline border, widest at midlength, distodorsally slightly concave, with few distal setae; 2 large basal statocysts present.

Antennular peduncle 3-segmented, basal segment equal in length to 3 distal segments; flagellum of 3 articles. Antennal peduncle 5-segmented, second segment grooved to accommodate antennule; flagellum of 2 articles. Mandibular palp 3-segmented, terminal segment short, bearing 2 setae, middle segment longest, with elongate distal seta; incisor of 2 blunt cusps; lamina dentata with 4 marginal serrations; molar distally bluntly bilobed. Maxilla slender with one strong spine

TABLE 24.—Distribution and morphological comparison of four species of *Apanthura*

	<i>A. magnifica</i>	<i>A. signata</i>	<i>A. signata</i>	<i>A. geminsula</i>
Distribution	Georgia to Florida	Puerto Rico; Belize	Venezuela	Belize
Pigment	absent	present	absent	absent
Dorsal pits	slight depression on pereonites 4–6	slight depression on pereonites 4–6	slight depression on pereonites 4–6	marked pits on pereonites 4–6
Antennular flagellum basal article ♀	elongate	short	elongate	short
Antennal flagellum articles	4	3	3	2
Maxillipedal endite	present	present	absent	present
Uropodal endite	notched	notched	unnotched	notched
Size ♀	8.5 mm	4.5 mm	5.0 mm	8.1 mm

and 5 smaller distally curved spines. Maxilliped 5-segmented, terminal segment situated on outer distal angle of fourth segment, with 5 setae; third segment narrowed, less than half length of fourth segment; slender endite on inner surface with single terminal seta. Pereopod 1 unguis almost half length of dactylus; propodal palm with few simple spines, rounded hyaline lobe at about midpoint: carpus triangular, distally narrowed. Pereopods 2 and 3 considerably smaller than pereopod 1. Posterior pereopods with propodus having strong posterodistal spine and several small fringed scales on posterior margin; carpus small, triangular, underriding propodus, with strong posterodistal spine. Pleopod 1 exopod operculiform, distal margin bearing several plumose setae; endopod slightly shorter and about half width of exopod, with few distal plumose setae. Uropodal exopod distally notched, extending to distal end of basis; endopod extending beyond telsonic apex, distally rounded, bearing numerous simple setae.

**DESCRIPTION OF MALE.**—Eyes considerably larger than those in female. Antennular flagellum of 8 or 9 articles, each bearing whorl of filiform aesthetascs. Mandibular palp as in female, but incisor, lamina dentata, and molar reduced to blunt nonsclerotised lobes. Pereopod 1 with hyaline process at about midpoint of propodal palm narrower than in female; numerous simple spines on medial margin; carpus with narrowly rounded hyaline posterodistal lobe. Pleopod 2 endopod

with cylindrical, apically narrowly rounded copulatory stylet extending beyond apices of rami.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble, coarse sediments, 0.2–1.5 m; Twin Cays, under mangroves, 0.2 m.

*Holotype:* ♀ (TL 8.1 mm), Twin Cays, USNM 171166.

*Allotype:* ♂ (TL 4.8 mm), Twin Cays, USNM 171167.

*Paratypes:* 3♂, 3♀, Twin Cays, USNM 171168.

*Additional Material:* 120♀, 3 sub♂, 7♂, 50 juveniles.

**REMARKS.**—Superficially the species of the genus *Apanthura* are all remarkably similar, but subtle differences are to be found in the mandibular palp spination-setation, telsonic shape, maxillipedal segment proportions, and in the structure of the first maxillipeds. *Apanthura magnifica* Menzies and Frankenberg (1966), *A. signata*, and *A. signata* Paul and Menzies (1971) have been recorded either from the Caribbean or from adjoining areas, and are all figured as having pleonites 1–3 free, and pleonites 4 and 5 dorsally fused. Clearing specimens of *A. magnifica* and *A. geminsula* in lactic acid and Chlorozol Black shows that pleonites 1–5 are dorsally fused, but that pleonites 1–3 have a groove or fold over the dorsum which appears as an articulation. Careful examination of the type material of *A. signata* and *A. signata* shows a similar fusion. The main distinguishing features of the four species of *Apanthura* discussed here are summarized in Table 24.

**ETYMOLOGY.**—The specific name *geminsula* is a Latinized form of Twin Cays, the locality where the species was abundant.

### *Apanthura signata* Menzies and Glynn

FIGURE 143

*Apanthura signata* Menzies and Glynn, 1968:28, fig. 10.—Paul and Menzies, 1971:42.

**DESCRIPTION OF FEMALE.**—Body hardly indurate. Body proportions:  $C < 1 = 2 > 3 < 4 < 5 > 6 > 7$ . Pereonites 4, 5, and 6 with shallow middorsal depression. Pleonites 1–5 dorsally fused, laterally distinct; pleonite 6 free. Telson not indurate, gently convex dorsally with relatively broad hyaline border, widest at midpoint; with 2 proximal statocysts.

Antennular peduncle 3-segmented, basal segment slightly shorter than 2 distal segments together; flagellum of 3 articles, second article relatively elongate. Antennal peduncle 5-segmented, flagellum of 3 articles. Mandibular palp 3-segmented, terminal segment with 3 terminal setae, first and second segments each with single elongate seta; incisor of 3 blunt cusps, lamina dentata with 5 marginal serrations, molar blunt. Maxilliped 5-segmented, with thin-walled endite on inner surface. Pereopod 1 unguis almost half the length of dactylus; propodal palm with rounded distal lobe and convex hyaline flange, few simple setae; carpus triangular, posterodistal angle produced, narrowly rounded. Posterior pereopods with triangular carpus bearing strong posterodistal spine. Pleopod 1 exopod operculiform, endopod more than half as wide and almost as long as exopod. Uropodal exopod notched, extending beyond basis.

**DESCRIPTION OF SUBMALE.**—Eyes larger than in female, but not as large as in mature male. Antennular flagellum lacking filiform aesthetascs.

**DESCRIPTION OF MALE.**—Cephalon with eyes much larger than in female. Antennular flagellum of 9 articles bearing filiform aesthetascs. Mandible with palp as in female, but incisor, lamina dentata, and molar somewhat reduced. Pereopod 1 with propodal palm having low

rounded process at about midpoint, hyaline convex flange on inner surface shorter than in female, but with more setae than in female. Pleopod 2 endopod with cylindrical, distally rounded copulatory stylet extending well beyond rami.

**COLOR NOTES.**—Pigment pattern fairly regular, especially the dark band between eyes and narrow bands on anterior and posterior dorsal parts of pereonites, and on pleonite 6 in female. Pigmentation in male lacking regularity found in female; chromatophores scattered over dorsal and ventral surfaces.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble and coarse sediments, intertidal to 24 m: ~ 120♀, 2 sub♂, 7♂, 25 juveniles.

**PREVIOUS RECORDS.**—Puerto Rico.

### *Apanthuroides* Menzies and Glynn

#### *Apanthuroides millae* Menzies and Glynn

FIGURES 144, 145

*Apanthuroides millae* Menzies and Glynn, 1968:30, fig. 11.

**DESCRIPTION OF FEMALE.**—Integument hardly indurate, with numerous pits on cephalon, pereon, pleon, and telson, and fine scales (seen with difficulty). Body proportions:  $C < 1 > 2 = 3 = 4 = 5 > 6 > 7 < P$ . Cephalon with short triangular rostrum not extending as far as anterolateral corners. Eyes dorsolateral. Pereonite 7 very short, one-third length of 6. Pleonites 1–5 fused, with shallow grooves indicating lines of fusion; pleonite 6 fused with telson. Latter proximally broad, distal two-thirds narrowed, apically rounded, with strong middorsal longitudinal ridge.

Antennular peduncle 3-segmented, basal segment broad, equal in length to 2 distal segments plus 2 basal flagellar article; flagellum of 4 articles, two distal articles each with single aesthetasc. Antennal peduncle 5-segmented, second segment grooved to accommodate antennule; flagellum of 7 articles. Mandibular palp 3-segmented, middle segment broadest and longest, terminal segment with 3 distal finely fringed spines; incisor of 2 blunt cusps, narrow lamina dentata with 6 or 7

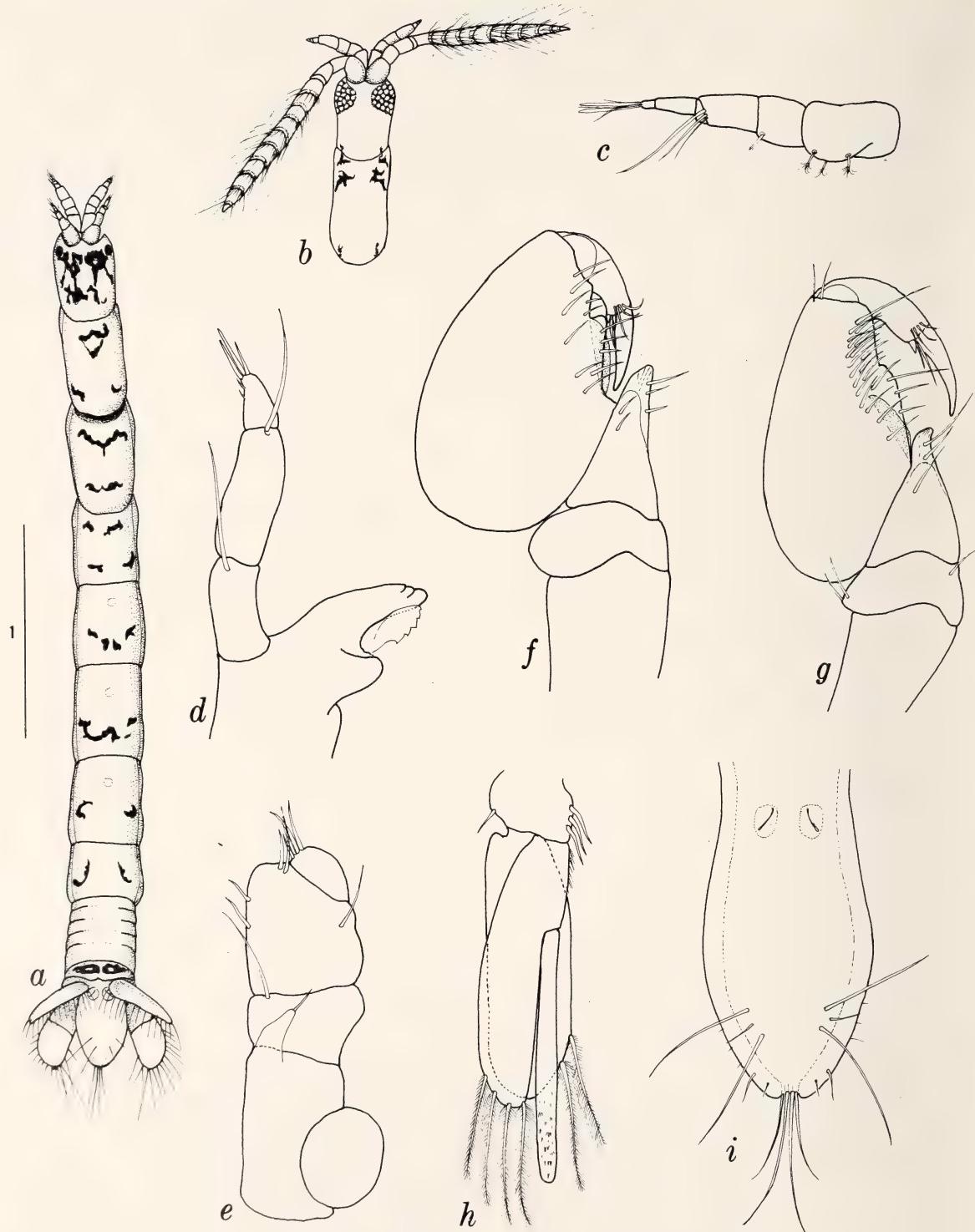


FIGURE 143.—*Apanthura signata* Menzies and Glynn: *a*, complete specimen, ♀; *b*, cephalon, ♂; *c*, antennule ♀; *d*, mandible; *e*, maxilliped; *f*, pereopod 1, ♀; *g*, pereopod 1, ♂; *h*, pereopod 2, ♂; *i*, telson.

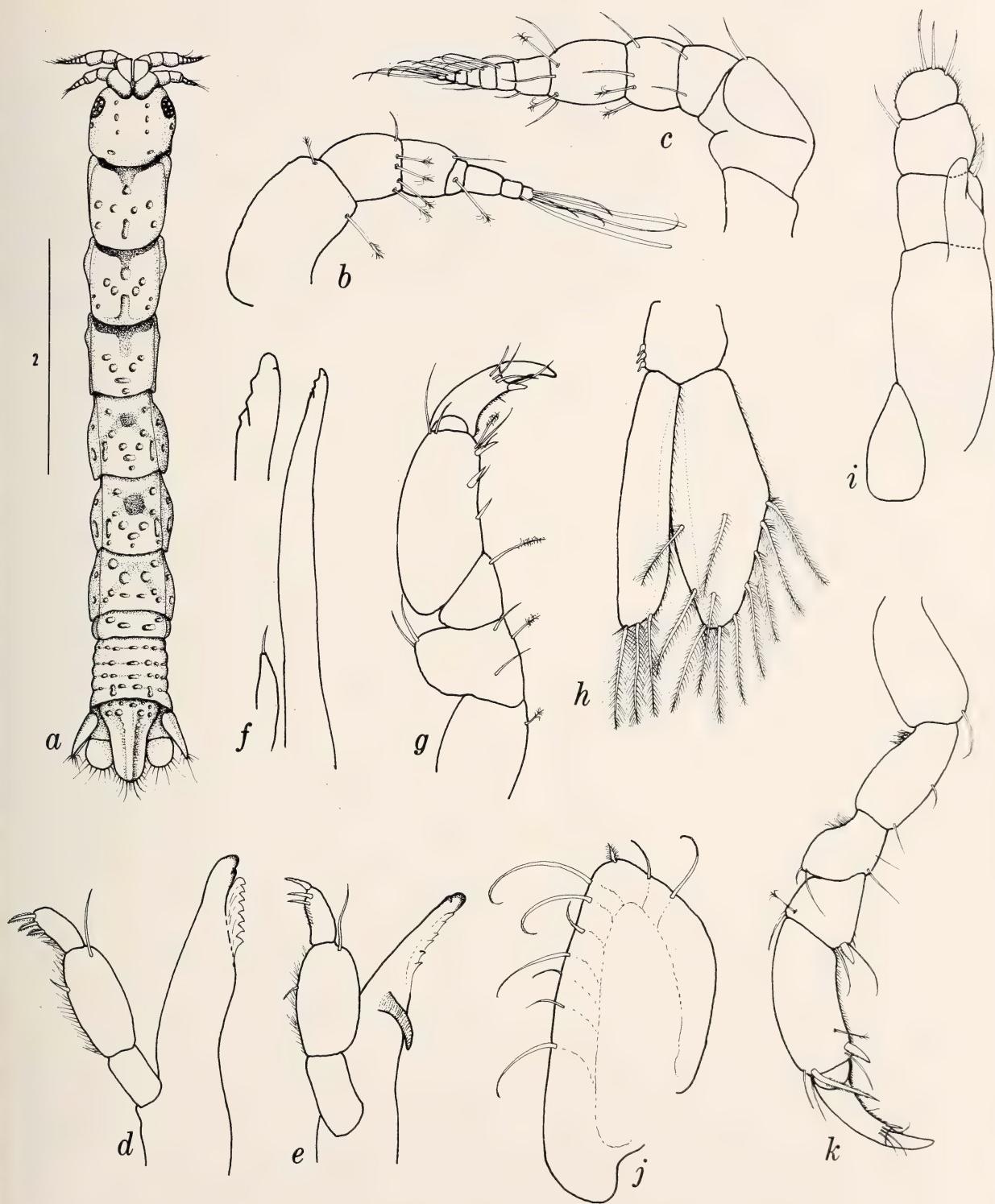


FIGURE 144.—*Apanthuroides millae* Menzies and Glynn, holotype, ♀: *a*, complete specimen; *b*, antennule; *c*, antenna; *d*, left mandible; *e*, right mandible; *f*, maxilla; *g*, pereopod 1; *h*, pleopod 1; *i*, maxilliped; *j*, uropodal exopod; *k*, pereopod 6.

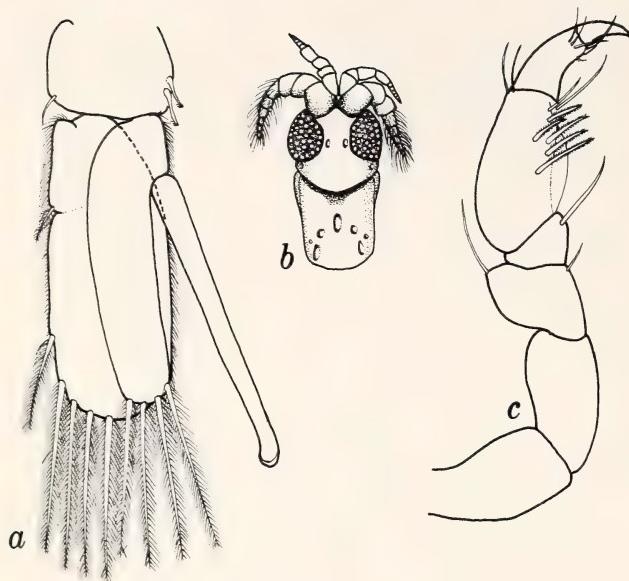


FIGURE 145.—*Apanthuroides millae* Menzies and Glynn, ♂: *a*, pleopod 2; *b*, cephalon; *c*, pereopod 1.

serrations; molar of right mandible elongate, slender, finely ridged, absent on left mandible. Maxilla elongate, slender, apically with 3 or 4 broadened cusps, no spines distinguishable. Maxilliped 5-segmented, terminal segment semicircular, setose, second segment elongate, with well-developed thin-walled endite on inner face. Pereopod 1 not markedly larger than following pereopods; unguis one-third length of dactylus, with short basal spine; propodus not very broad, palm straight, with 3 spines. Posterior pereopods, propodus with 2 distal finely-fringed spines; carpus slightly underriding propodus, anterior margin somewhat shorter than posterior margin; latter with strong posterodistal spine. Pereopod 7 absent. Pleopod 1 exopod twice width and subequal in length to endopod, rami overlapping slightly, together forming opercular surface closing off branchial chamber. Uropodal exopod extending well beyond basis, twice as long as wide, distally rounded, margin entire, sparsely setose; endopod almost circular, sparsely setose.

**DESCRIPTION OF MALE.**—Integument somewhat less pitted than in female. Eyes enlarged. Antennular flagellum with 6 or 7 articles bearing

filiform aesthetascs. Propodus of pereopod 1 with thin convex flange along palm, latter with 5 finely fringed spines in distal half. Pleopod 2 endopod with cylindrical copulatory stylet, apically rounded.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coarse sediments, 6–24 m: 3♀ (TL 2.3–2.8 mm), 1♂ (TL 2.8 mm), USNM 171154.

**REMARKS.**—The type material of this species, consisting of two males from Puerto Rico, agrees well with the male of the present material. Menzies and Glynn (1968), in describing *A. millae*, neither figured nor mentioned the characteristically pitted integument, neither did they figure the unusual mandible.

Several features of this species agree with *Natalanthura foveolata* Kensley, 1978a, described from the southwest Indian Ocean. These similarities include the pitted integument, the 5-segmented maxilliped with endite, the elongate mandible with a slender molar present only on one side, pelopod 1 with the exopod and endopod together forming an operculum over the branchial chamber, and pleonites 1–5 fused, pleonite 6 fused with the telson. (With regard to the latter feature, Kensley (1978a) described the pleon of *N. foveolata* as having pleonites 1–3 free, 4 and 5 fused, 6 fused with the telson. Clearing of a specimen with lactic acid and Chlorozol Black has shown that pleonites 1–5 are completely fused, as in the present species). The aforementioned features, especially the unique mandibular structure, leave no doubt that *Natalanthura* should be regarded as a junior synonym of *Apanthuroides*.

### ***Belizeanthura*, new genus**

**DIAGNOSIS.**—Eyes present. Antennal flagellum of 7 articles. Mandibular palp 3-segmented; incisor, lamina dentata, and molar reduced in ♂, normal in ♀. Maxilliped 7-segmented with endite in ♀; 5-segmented and lacking endite in ♂. Pereopods 1–3 similar, subchelate. Pereopods 4–7 with triangular carpus underriding propodus. Pleopod 1 not operculiform. Pleonites 1–6 free. Telson lacking statocysts.

TABLE 25.—Comparison of anthurid genera possessing a seven-segmented maxilliped

Character	<i>Neohyssura</i>	<i>Ocsanthura</i>	<i>Minyanthura</i>	<i>Belizanthura</i>
Eyes	absent	absent	present	present
♂ mouthparts	?	similar to ♀	similar to ♀	very reduced
Carpus of pereopods 4–7	triangular	rectangular	rectangular	triangular
Pleopod 1	non-operculiform	non-operculiform	operculiform	non-operculiform
Pleonites	1–5 free, 6 fused with telson	1–6 free	1–5 fused, 6 fused with telson	1–6 free
Telson	spiniform	flattened	flattened	flattened
Statocysts	?	2	2	absent

TYPE-SPECIES.—*Belizanthura imswe*, new species.

ETYMOLOGY.—The generic name is derived from the country of Belize, plus *anthura*, the suffix often used for anthurid genera.

REMARKS.—A 7-segmented maxilliped as in the female of *Belizanthura* also occurs in *Neohyssura* Amar (1952), *Ocsanthura* Kensley (1978b), and *Minyanthura*, new genus. The features separating these genera are summarized in Table 25.

### *Belizanthura imswe*, new species

FIGURES 146, 147

DESCRIPTION OF FEMALE.—Body very slender, semi-transparent when alive, integument thin, not indurate. Body proportions: C > 1 < 2 = 3 < 4 = 5 > 6 > 7. Cephalon with low triangular rostrum, tiny dorsal eyes. Pleonites free, 1–5 subequal, 6 with notch in posterodorsal margin. Telson widest at midlength, tapering to rounded setose apex, lateral margins distally with 7 or 8 shallow serrations; statocysts absent.

Antennular peduncle 3-segmented, flagellum of 4 articles, terminal article tiny. Antennal peduncle 5-segmented; flagellum of 7 articles. Mandibular palp 3-segmented, middle segment twice length of first, third segment bearing 3 distal fringed setae; incisor of 3 cusps; lamina dentata with 4 serrations and several tiny spinules; molar bluntly rounded. Maxilla with one large and 4 small distal spines. Maxilliped 7-segmented, terminal segment small, with 3 setae; third segment short; endite reaching to distal margin of fourth

segment, thin-walled, with single terminal seta. Pereopods 1–3 similar, unguis half length of dactylus; propodal palm very slightly sinuous, with few scattered setae; carpus triangular, with posterodistal point. Posterior pereopods with unguis about one-quarter length of dactylus, propodus with 3 posterodistal sensory spines; carpus almost triangular, with short free anterior margin. Pleopod 1 not operculiform, subequal to following pleopods. Uropodal exopod pyriform, basally broad, outer margin with 4 or 5 serrations, distally rounded, setose; endopod longer than basis, extending slightly beyond telson, distally rounded, setose.

DESCRIPTION OF MALE.—Antennular flagellum of 8 articles, each with whorl of filiform aesthetascs. Eyes enormously enlarged, almost meeting middorsally and midventrally, with just sufficient space between to accommodate mandibular palps; remainder of mandible reduced to short nonmasticatory segment. Maxillae absent. Maxilliped 5-segmented, only terminal segment bearing 3 setae; endite absent. Pereopod 1 unguis about one-third length of dactylus; propodal palm straight, armed with about 8 short, fringed spines; carpus triangular, with apical fringed spine and short, acute process. Pereopod 2 propodus slightly shorter than pereopod 1, palm armed with 3 strong ventrodistal sensory spines. Posterior pereopods as in female. Pleopod 1 basis with 2 slender retinaculae, exopod and endopod subequal in length, broadly rounded distally both bearing elongate plumose setae. Pleopod 2 basis

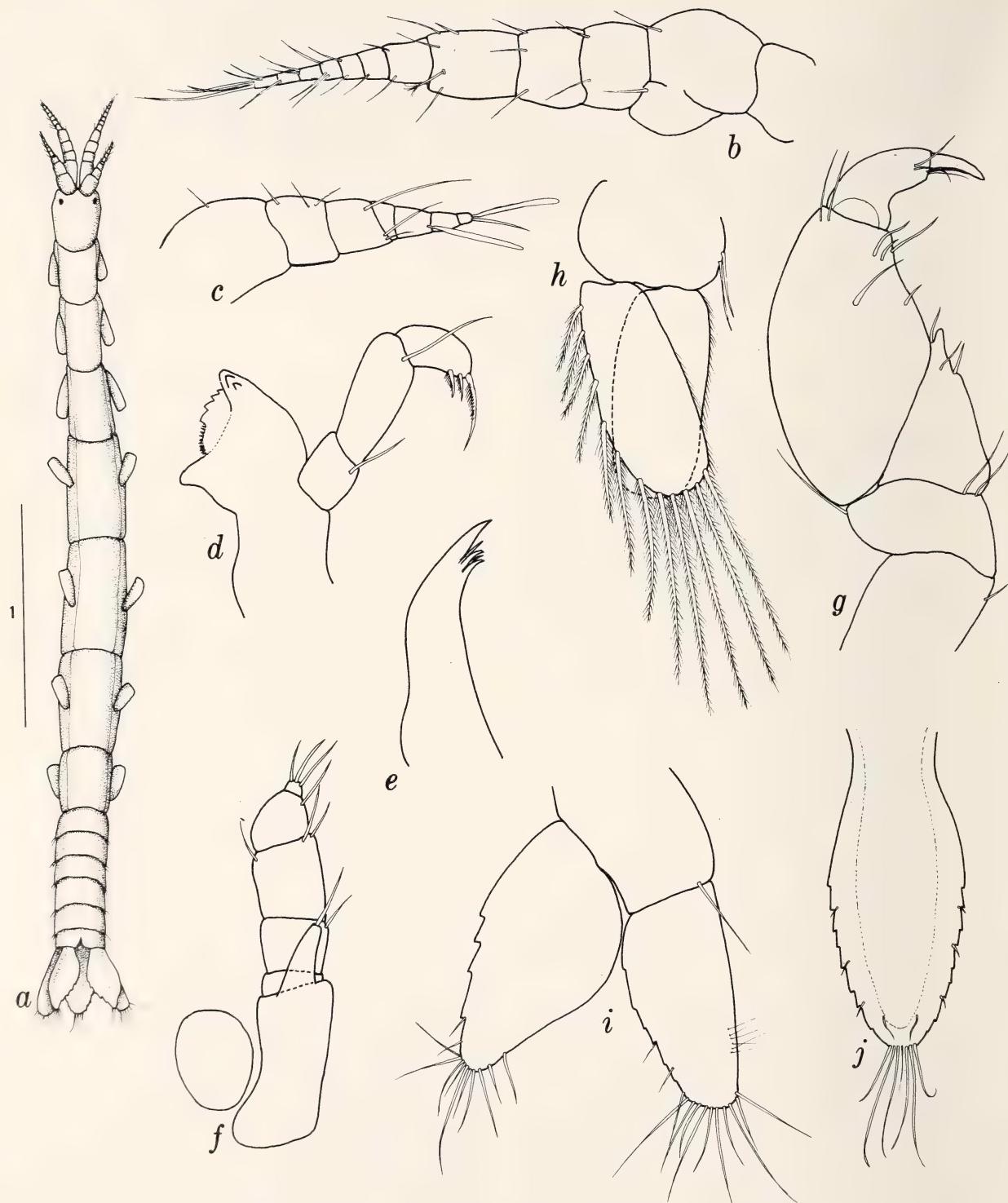


FIGURE 146.—*Belizanthura imswe*, new species, holotype, ♀: a, complete specimen; b, antenna; c, antennule; d, mandible; e, maxilla; f, maxilliped; g, pereopod 1; h, pleopod 1; i, uropod; j, telson.

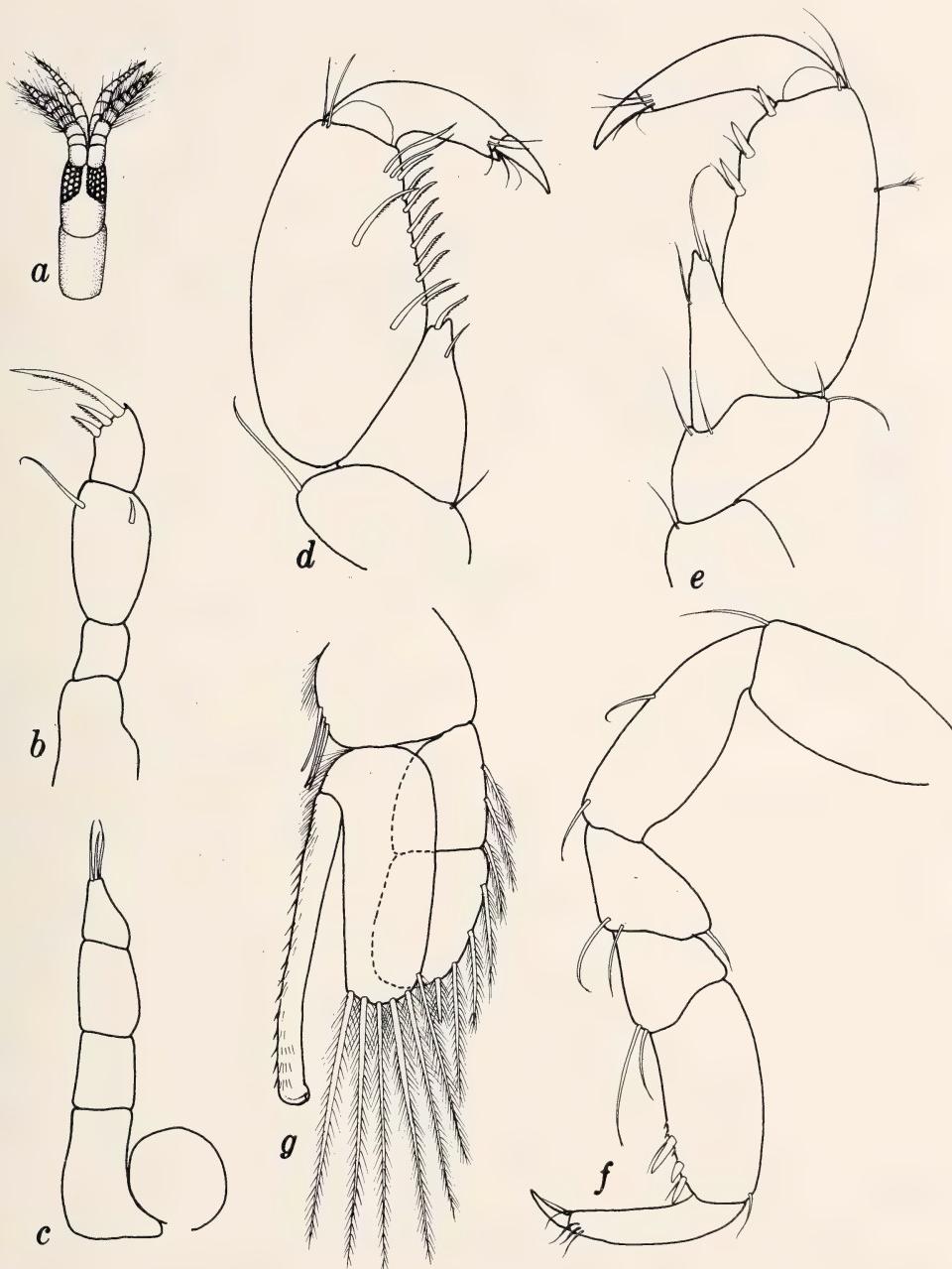


FIGURE 147.—*Belizanthura imswe*, new species, ♂: a, cephalon; b, mandible; c, maxilliped; d, pereopod 1; e, pereopod 2; f, pereopod 7; g, pleopod 2.

with 3 retinaculae; endopod bearing stout, apically rounded copulatory stylet extending well beyond ramus; exopod with distinct transverse suture at midlength.

MATERIAL EXAMINED.—Carrie Bow Cay, coral

rubble and shallow coarse sediments, 0.1–0.3 m; Twin Cays, in algal mat under mangroves, 0.1–0.3 m.

*Holotype*: ♀ (TL 3.4 mm), Twin Cays, USNM 171172.

Allotype: ♂ (TL 2.5 mm), USNM 171173.

Paratypes: 4♀ (TL 3.0–3.7 mm), 4♂ (TL 2.3 mm–2.7 mm), Twin Cays, USNM 171174.

Additional Material: 27♀, 2♂.

ETYMOLOGY.—The specific name is the acronym for “Investigations of Marine Shallow Water Ecosystems.”

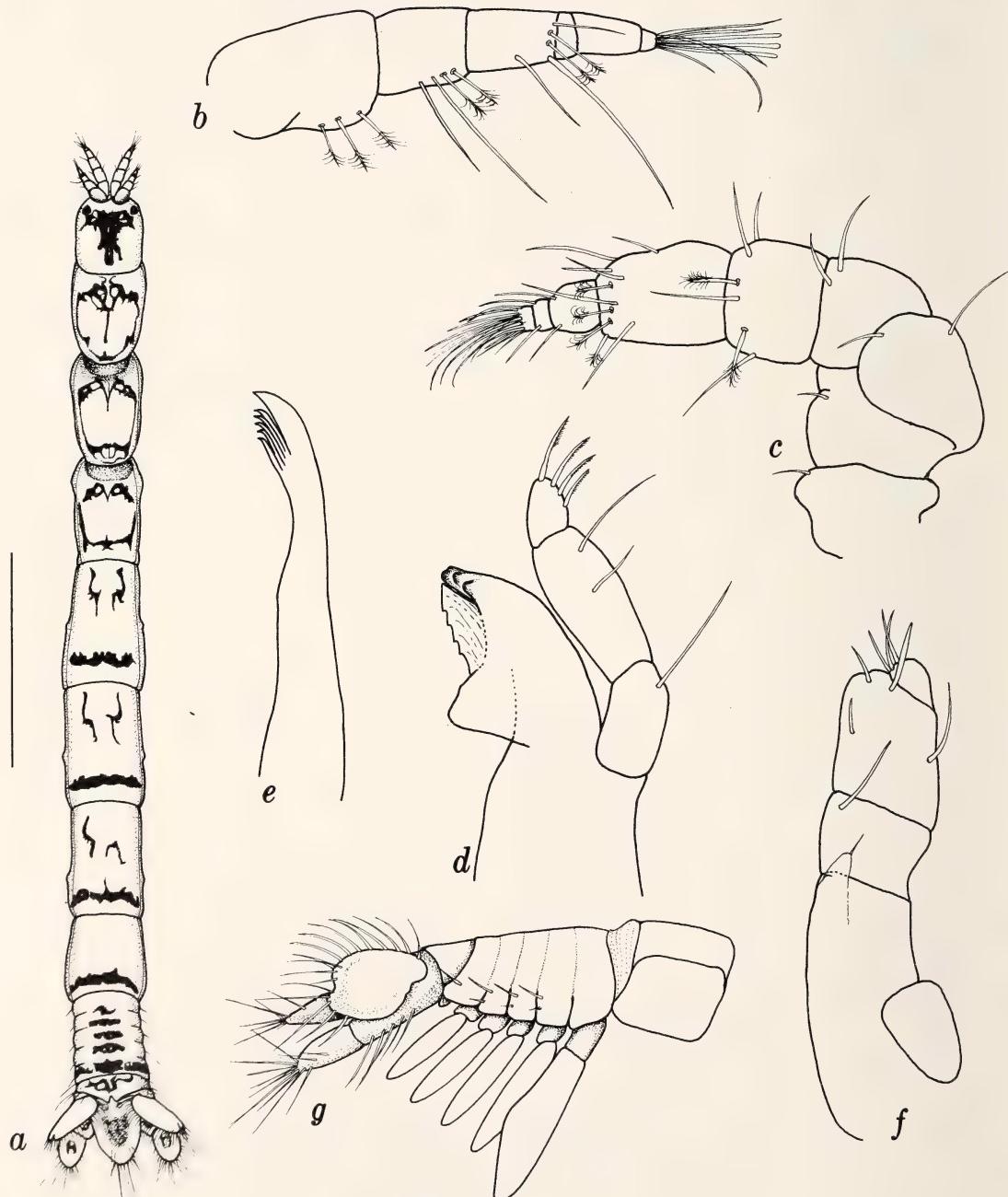


FIGURE 148.—*Mesanthura fasciata* new species, holotype, ♀: a, complete specimen; b, antennule; c, antenna; d, mandible; e, maxilla; f, maxilliped; g, pleon in lateral view.

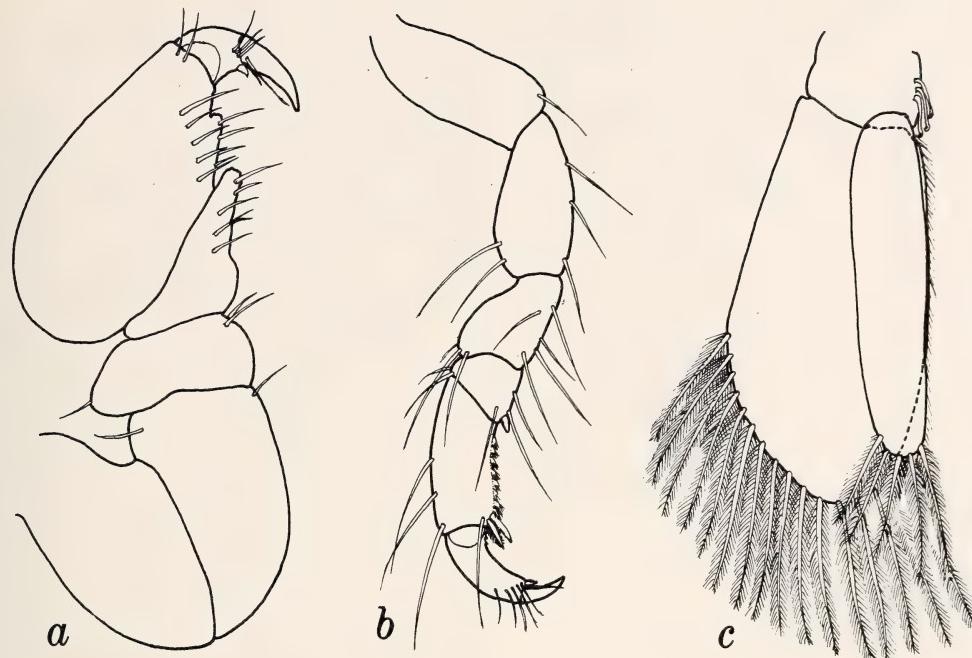


FIGURE 149.—*Mesanthura fasciata* new species, ♂: *a*, pereopod 1; *b*, pereopod 7; *c*, pleopod 1.

### *Mesanthura*, Barnard

#### *Mesanthura fasciata*, new species

FIGURES 148, 149

**DESCRIPTION OF FEMALE.**—Integument not indurate. Body proportions:  $C < 1 < 2 = 3 < 4 = 5 > 6 > 7$ . Cephalon with low rostrum, not extending beyond anterolateral corners; eyes dorsolateral. Pereonites 2 and 3 each with anterodorsal hollowed area. Pleonites 1–5 fused, indicated laterally, and with dorsal grooves marking fusion lines; pleonite 6 free, with middorsal notch in posterior margin. Telson dorsally slightly convex, distal margin rounded.

Antennular peduncle 3-segmented, flagellum 3-segmented, distal segment one-quarter length of second segment, with 3 aesthetascs. Antennal peduncle 5-segmented, second segment grooved to accommodate antennule; flagellum 3-articulate. Mandibular palp 3-segmented, third segment one-third length of second, with 4 finely fringed spines; incisor of 3 cusps; lamina dentata with 4 serrations; molar bluntly rounded. Maxilla with 1 strong spine and 5 smaller distally curved

spines. Maxilliped 5-segmented, terminal segment small, set obliquely at outer distal angle of fourth segment; tiny thin-walled endite present at base of third segment. Pereopod 1 dactylus with small spine at base of unguis; propodal palm with rounded lobe at about midlength; 5 simple setae on inner face of propodus; carpus triangular, distally somewhat produced and rounded. Pereopods 2–7 similar; posterior pereopods with triangular carpus bearing short posterodistal spine, underriding propodus; latter with 2 serrate posterodistal spines; posterior margin bearing tiny fringed spines. Pleopod 1 exopod operculiform, extending somewhat beyond endopod; both rami with distal plumose setae; basis with 3 retinaculae. Uropodal exopod with strong distal notch, fringed with plumose setae, extending beyond base of endopod; latter oval, extending slightly beyond telsonic apex.

**COLOR NOTES.**—Red-brown pigment pattern constant, characterized by irregular patch on cephalon, delicate reticulation on pereonites 1–3; thin anterior submedian lines and posterior solid transverse bars on pereonites 4–7; pleon with 5 short transverse bars on fused pleonites 1–5,

pleonite 6 with fine middorsal tracery; patches of pigment on telson and uropodal bases and endopods.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble and coarse sediments, intertidal to 24 m.

**Holotype:** ♀ (TL 4.5 mm), Carrie Bow Cay, USNM 171162.

**Paratypes:** 6♀ (TL 3.7–4.5 mm), USNM 171163.

**Additional Material:** 28♀, 25 juveniles.

**REMARKS.**—On the basis of the color pattern, the present species bears some resemblance to *M. occidentalis* Menzies and Barnard, 1959, from southern California, especially in the delicate tracery on pereonites 1–3. The Californian species, however, lacks the strong posterior pigment bars on pereonites 4–7 and the 5 shorter bars on the pleon. The 2 species can further be separated on the form of the maxilliped.

**ETYMOLOGY.**—The specific name, derived from the Latin *fasciata* (striped), refers to the transverse bands of pigment on the posterior pereonites and on the pleon.

### ***Mesanthura paucidens* Menzies and Glynn**

FIGURES 150, 151

*Mesanthura paucidens* Menzies and Glynn, 1968:27, fig. 9A–G.

**DESCRIPTION OF FEMALE.**—Anterolateral lobes of cephalon rounded, not extending beyond rostrum. Cephalon with marked dorsolateral ridge; midventral margin posterior to maxilliped evenly convex. Pereon and pleon not indurate. Pleonites 1–5 fused, sutures barely discernible along ventrolateral margin; pleonite 6 free, with narrow middorsal notch in posterior margin. Telson dorsally gently convex, distal margin evenly rounded.

Antennular peduncle 3-segmented, distal segment very short, flagellum of 3 articles, terminal article bearing several setae and 2 aesthetascs. Antennal peduncle 5-segmented, second segment grooved to accommodate antennule; flagellum of 3 (?4) short setose articles. Mandibular palp 3-segmented, terminal segment shortest and narrowest, with 6 stout spines; incisor of 3 blunt cusps, linked to somewhat reduced and rounded

molar by 6-serrate lamina dentata. Maxilla slender, with 6 terminal spines. Maxilliped 5-segmented, second segment with reduced endite on inner face. Pereopod 1 unguis half length of dactylus; propodal palm finely crenulate, with small convex transparent process at midpoint bearing simple setae. Pereopod 2 unguis one-third length of dactylus; propodus cylindrical, with strong serrate distoventral spine; carpus triangular. Pereopods 5–7 with carpus and propodus each with distoventral spine. Pleopod 1 exopod operculiform, about 3 times width of endopod; basis with 4 retinaculae. Uropodal exopod (Figure 150e) distally sinuous rather than notched.

**DESCRIPTION OF MALE.**—Eyes larger than in female. Antennular flagellum of 7 articles, each with whorl of filiform aesthetascs. Pereopod 1 with lobe at about midpoint of propodal palm, inner surface of propodus with many finely serrate spines. Pleopod 2 copulatory stylet cylindrical, extending beyond rami, distally spinulose, apically rounded and slightly sclerotised.

**COLOR NOTES.**—Female with roughly rectangular dorsal patches of chromatophores on cephalon and pereonites. Pleon with 5 laterally linked transverse bars. Telson and uropodal endopod and basis with proximal chromatophores. Male with pigmentation of pereon heavier and less defined than in female, but with 5 pleonal bars as in female.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble and shallow sediments: 25♀ (TL 6.6 mm), 1♂ (TL 6.4 mm), 9 juveniles. Twin Cays, under mangroves: 1♀.

**PREVIOUS RECORDS.**—Puerto Rico.

**REMARKS.**—The palm of pereopod 1 has a definite rounded process at midlength, but as this is transparent, it may have been overlooked and therefore not figured by Menzies and Glynn (1968). The presence of a small maxillipedal endite is unusual in *Mesanthura*, but may be related to the relatively small body size, and the almost interstitial habit. The fact that the holotype is only about one-third the length of the present mature male and females may account for the omissions in the original description.

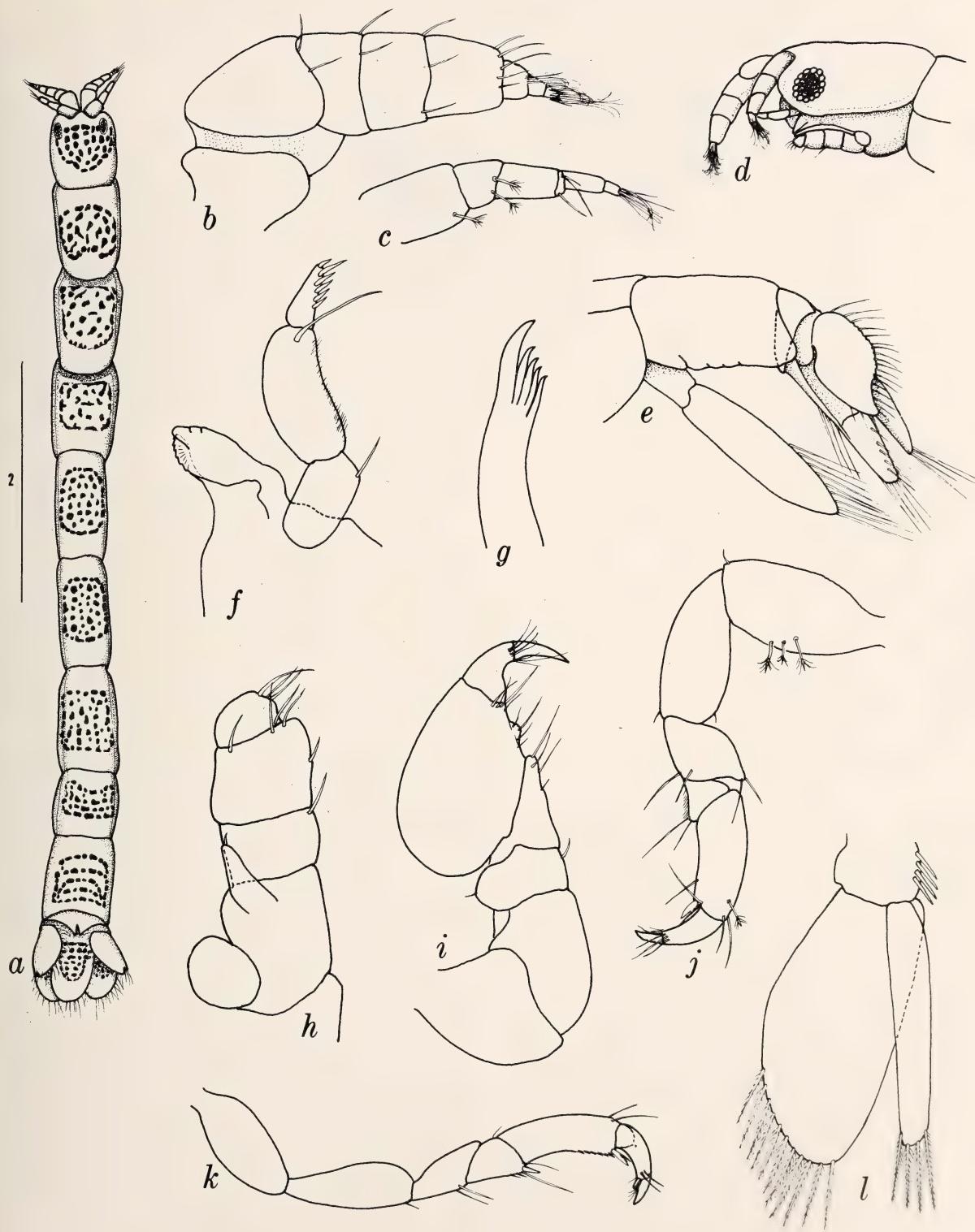


FIGURE 150.—*Mesanthura paucidens* Menzies and Glynn, ♀: *a*, complete specimen; *b*, antenna; *c*, antennule; *d*, cephalon in lateral view; *e*, pleon in lateral view; *f*, mandible; *g*, maxilla; *h*, maxilliped; *i*, pereopod 1; *j*, pereopod 2; *k*, pereopod 7; *l*, pleopod 1.

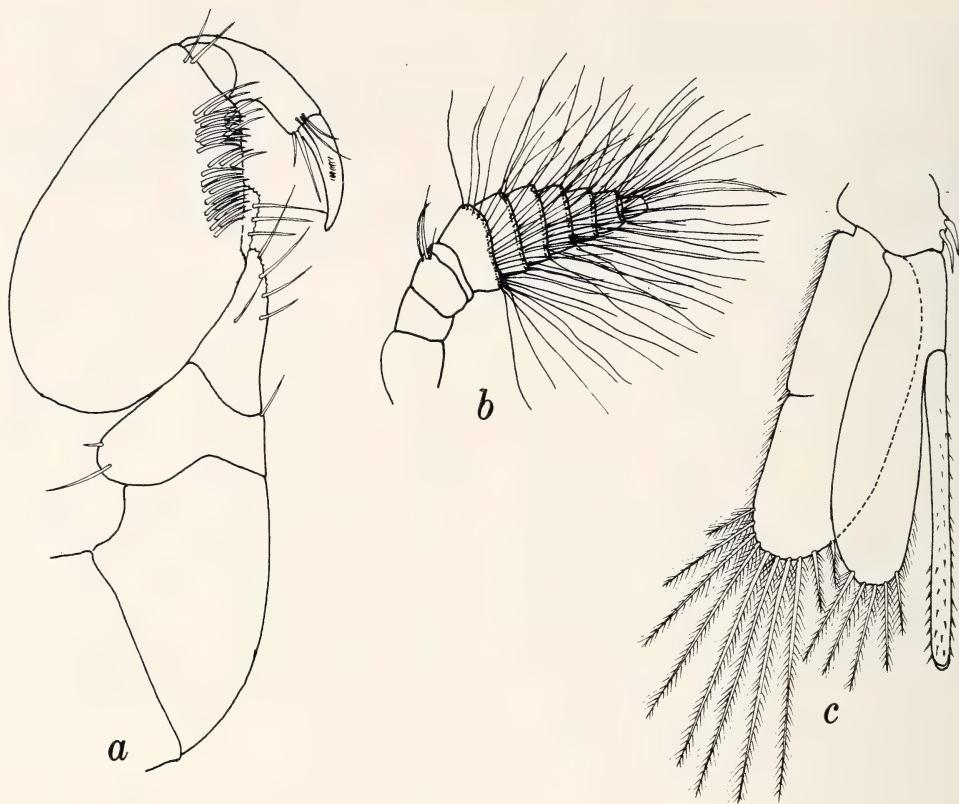


FIGURE 151.—*Mesanthura paucidens* Menzies and Glynn, ♂: a, pereopod 1; b, antennule; c, pleopod 2.

### *Mesanthura pulchra* Barnard

FIGURES 152, 153

*Mesanthura pulchra* Barnard, 1925:145, fig. 9e.—Schultz, 1969:109, fig. 151.

*Mesanthura decorata* Menzies and Glynn, 1968:26, fig. 8A-I.

**DESCRIPTION OF FEMALE.**—Cephalon with rostrum reaching as far forward as anterolateral angles. Body proportions:  $C < 1 = 2 > 3 < 4 = 5 = 6 > 7$ . Anterior 5 fused pleonites equal in length to pereonite 7; individual pleonites indicated by very short ventrolateral incisions; pleonite 6 free, with middorsal slit in posterior margin. Telson broadly rounded distally.

Antennular peduncle 3-segmented, basal segment longest and broadest, flagellum of 3 articles. Antennal peduncle 5-segmented, second segment broadest, hollowed dorsally to accommodate antennule; flagellum of 3 short articles. Mandibular palp 3-segmented, middle segment longest, distal

segment shortest, with row of 10 spines; incisor of 4 rounded cusps, linked to blunt rounded molar by lamina dentata having 5 serrations. Maxilla slender, with 5 or 6 distal spines. Lower lip bilobed, ending in narrowly rounded process, with fine lateral setae. Maxilliped 5-segmented, second segment longest; third segment slightly narrower than fourth; latter with 4 short setae on median margin; distal segment triangular, with 2 stout, fringed setae and few simple setae. Pereopod 1 unguis one-third length of dactylus; propodal palm with rounded process at about midpoint bearing row of 6 setae, remainder of propodus and carpus with few scattered setae. Pereopod 2 unguis one-quarter length of dactylus; propodus with distoventral spine and few setae; carpus very short, triangular. Pereopods 5-7, propodus with distoventral simple spine plus fringed spine and several short spinules; carpus triangular, under-riding propodus, with distoventral simple spine.

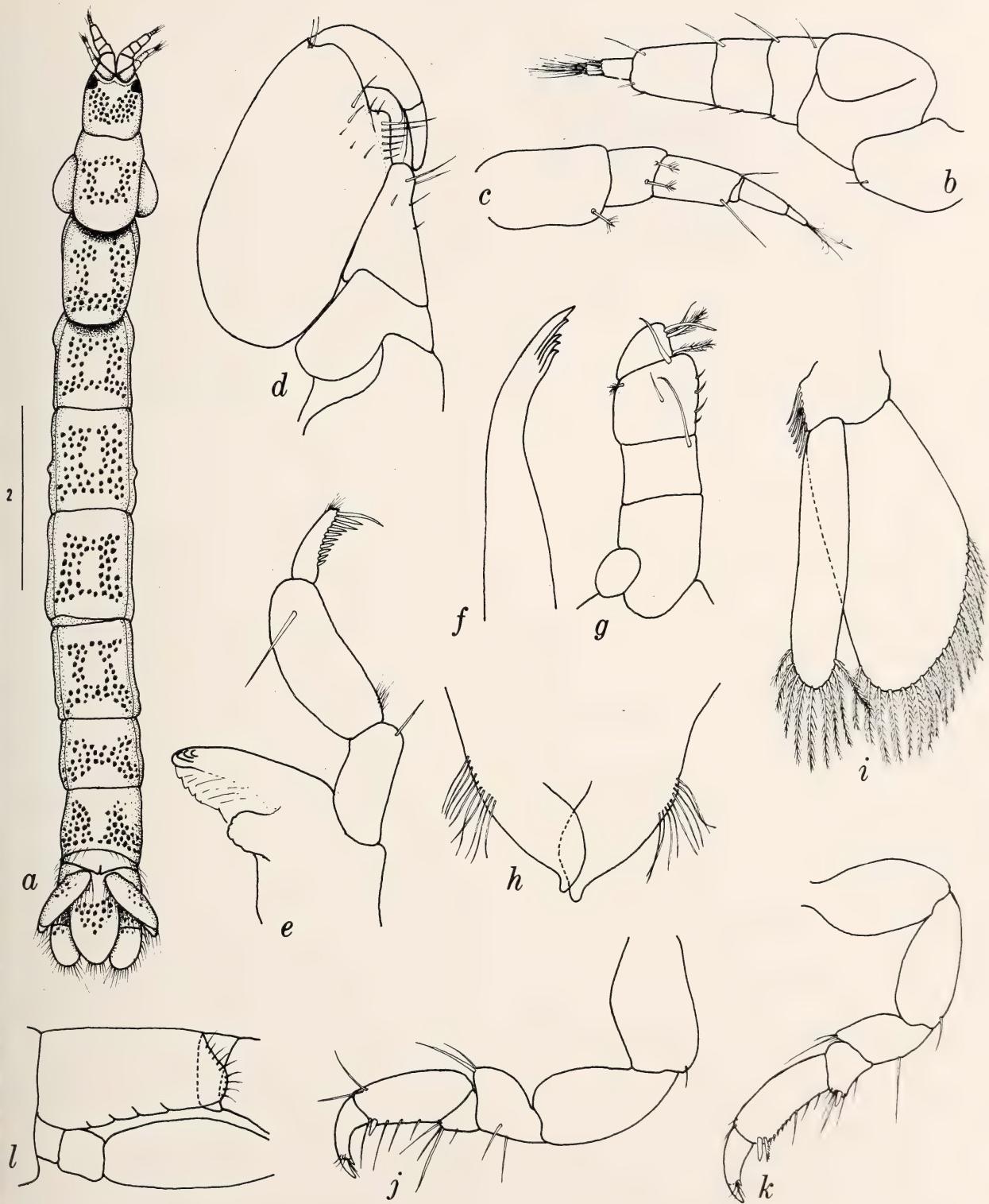


FIGURE 152.—*Mesanthura pulchra* Barnard, ♀: *a*, complete specimen; *b*, antenna; *c*, antennule; *d*, pereopod 1; *e*, mandible; *f*, maxilla; *g*, maxilliped; *h*, lower lip; *i*, pleopod 1; *j*, pereopod 2; *k*, pereopod 7; *l*, pleon in lateral view.

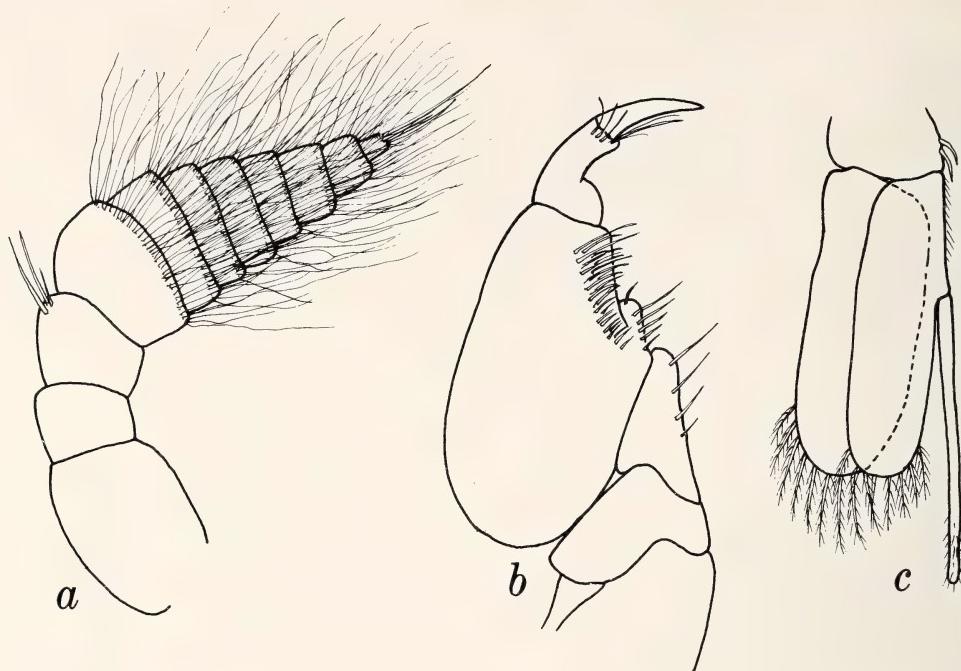


FIGURE 153.—*Mesanthura pulchra* Barnard, ♂: *a*, antennule; *b*, pereopod 1; *c*, pleopod 2.

Pleopod 1 exopod operculiform, 3 times width of endopod, with numerous plumose setae on distal margin; endopod with 9 plumose setae on distal margin; basis with 6 retinaculae. Uropods typical of genus.

**DESCRIPTION OF MALE.**—Antennule with 3-segmented peduncle, flagellum of 7 articles, each bearing whorl of filiform aesthetascs. Pereopod 1 similar to female, but with unguis half length of dactylus, propodus with dense band of spines on inner face of palm. Pleopod 2 copulatory stylet of endopod simple, cylindrical, extending well beyond rami.

**COLOR PATTERN.**—Broad band of chromatophores on cephalon posterior to eyes; hollow, roughly rectangular dorsal patch on pereonites 1–6, pereonite 7 and pleon with pigment band laterally broad, narrowed middorsally. Scattering of chromatophores on telson and uropods.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble and shallow sediments: 12♀ (TL 9.3 mm), 4 juveniles.

**PREVIOUS RECORDS.**—St. Thomas and St. John,

U.S. Virgin Islands; Puerto Rico; Dry Tortugas, Florida.

**TYPE MATERIAL.**—Barnard's type series from the Copenhagen Museum consists of 2♂ and 1 ovigerous ♀ syntypes, St. Thomas and St. John, 10–18 fathoms (18–33 m); ovigerous ♀ lectotype (TL 6.5 mm); 2♂ (TL 5.4 mm, 4.7 mm) paratypes.

**REMARKS.**—Although Barnard described this species in 1925, examination of the 3 type specimens still reveals the pigment pattern quite clearly. Menzies and Glynn (1968) based their species *M. decorata* on differences in the pigment patterns but made no comparison of appendages. Comparison of the Carrie Bow Cay material and that from the Dry Tortugas, Barnard's types, and Menzies and Glynn's types shows that despite slight differences (for example, in the presence or absence of a clear area on the cephalon), the basic pigment pattern is the same. Comparison of the appendages, especially the first pereopods in both the male and female shows no differences in the 4 groups of specimens available. Schultz's figure

(1969, fig. 151) misrepresents the pigment pattern.

### *Mesanthura punctillata*, new species

FIGURES 154, 155

**DESCRIPTION OF FEMALE.**—Integument moderately indurate. Cephalon with large dorsolateral eyes, low triangular rostrum extending slightly beyond anterolateral corners. Body proportions:  $C < 1 = 2 > 3 < 4 = 5 > 6 > 7$ . Pleonites 1–5 fused, only pleonite 1 indicated laterally; pleonite 6 free, with middorsal slit in posterior margin. Telson broadly rounded distally. Antennular peduncle 3-segmented, flagellum of 3 articles. Antennal flagellum 3-articulate. Mandibular palp 3-segmented, middle segment twice length of distal segment, latter armed with 7 finely fringed spines; incisor with 3 cusps; lamina dentata with 5 blunt marginal serrations; molar acute, slightly sclerotised. Maxilla with 1 strong and 4 smaller spines. Maxilliped 5-segmented, distal segment semicircular, with 4 setae; penultimate segment with 2 medial distal setae. Pereopod 1 unguis half length of dactylus, with tiny spine at base; propodus proximally broad, palm with hyaline serrate lobe at midlength; carpus narrowly triangular, distal rounded part bearing 5 serrations. Posterior pereopods with short triangular carpus underriding propodus; posterior margin of propodus bearing short, fringed scales; posterodistal corner with 1 simple and one serrate spine. Pleopod 1 exopod operculiform, about 3 times wider than endopod; both rami with distal plumose setae; basis with 4 retinaculae. Uropodal exopod with outer sinuous margin, but not notched; endopod almost circular.

**DESCRIPTION OF SUBMALE.**—Antennular flagellum elongate and swollen, but lacking aesthetascs. Pereopod 1 as in female. Pleopod 2 not yet differentiated.

**DESCRIPTION OF MALE.**—Eyes larger than in female, extending dorsally and ventrally. Antennule with flagellum of 10 articles bearing whorls of filiform aesthetascs. Mandible with palp as in

female; incisor and lamina dentata reduced and not sclerotised; molar absent. Pereopod 1 as in female but with dense band of simple spines on inner face of propodus. Pleopod 2 endopod with copulatory stylet extending well beyond rami, apically rounded.

**COLOR NOTES.**—Female with pigment pattern consisting of almost solid red-brown bar between eyes and extending in lobes posteriorly; pereon, pleon, telson, and uropods bearing scattered and separate pigment spots. (When chromatophores are expanded, pigment pattern is still scattered and does not become reticulate.) Male with chromatophores scattered dorsally and ventrally over entire body, denser than in female and with no discernible pattern.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble, coarse sediments, intertidal to 12 m.

*Holotype:* Ovigerous ♀ (TL 6.4 mm), Carrie Bow Cay, USNM 171157.

*Allotype:* ♂ (TL 4.5 mm), Carrie Bow Cay, USNM 171158.

*Paratypes:* ♂ (TL 4.5 mm), Carrie Bow Cay, USNM 171159; 3♀ (TL 5.7 mm, 5.2 mm, 5.2 mm), Carrie Bow Cay, USNM 171160.

*Additional Specimens:* 5♀, 2 sub♂, 8 juveniles.

**REMARKS.**—The distinctive pigment pattern distinguishes this species from its congeners from the same area. Other differences may be seen in the number of mandibular palp spines, shape of the uropodal exopod, the degree of lateral indication of the fusion of pleonites 1–5, and the armature of the first pereopod.

**ETYMOLOGY.**—The specific name *punctillata*, derived from the Latin word for small spots, refers to the overall scattered spots of pigment.

### *Mesanthura reticulata*, new species

FIGURE 156

**DESCRIPTION OF FEMALE.**—Integument hardly indurate. Body proportions:  $C = 1 < 2 = 3 = 4 < 5 > 6 > 7$ . Cephalon with dorsolateral eyes; tiny triangular rostrum. Pleonites 1–5 fused; 6 free, with middorsal notch in posterior margin.

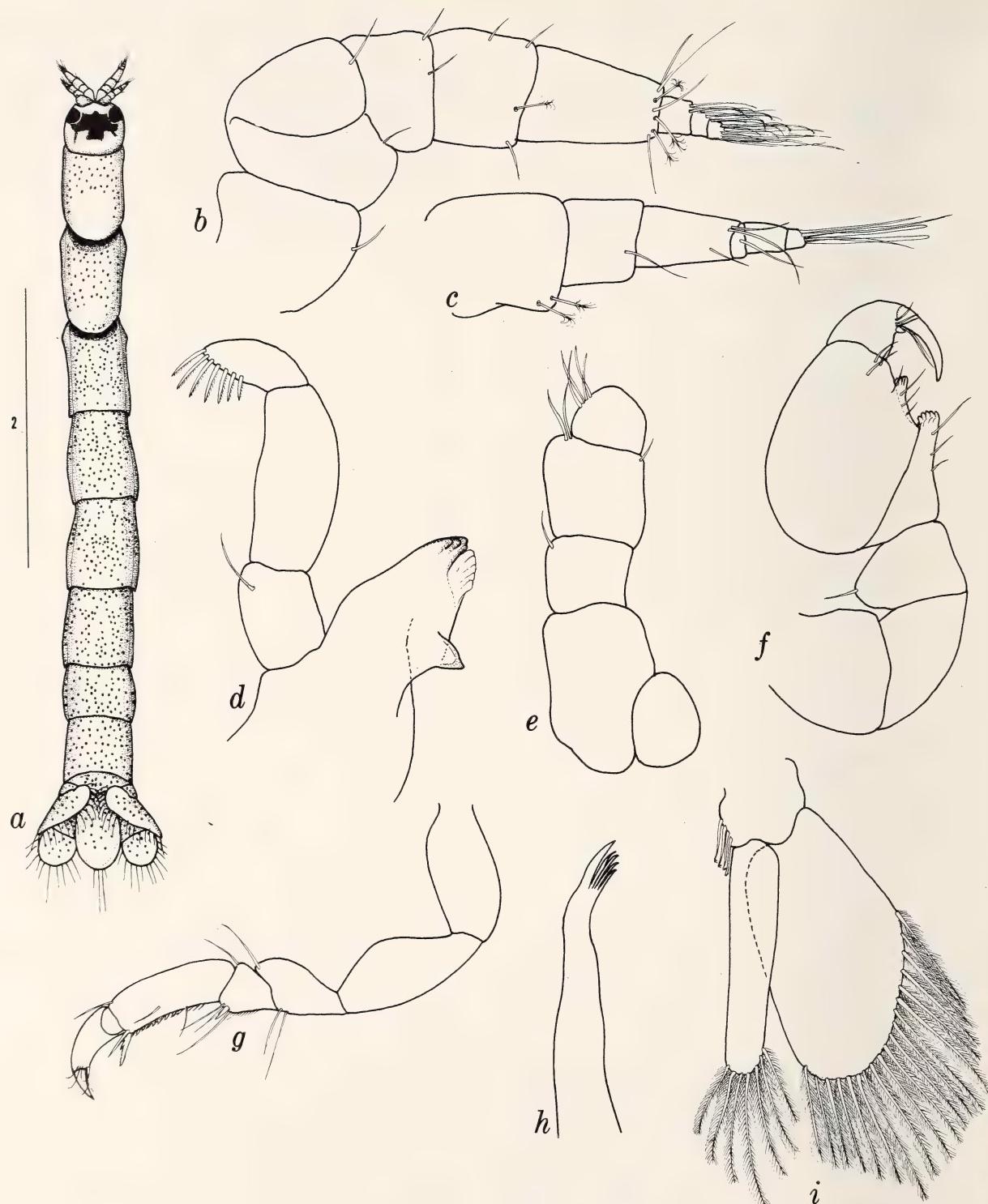


FIGURE 154.—*Mesanthura punctillata* new species, holotype, ♀: a, complete specimen; b, antenna; c, antennule; d, mandible; e, maxilliped; f, pereopod 1; g, pereopod 7; h, maxilla; i, pleopod 1.

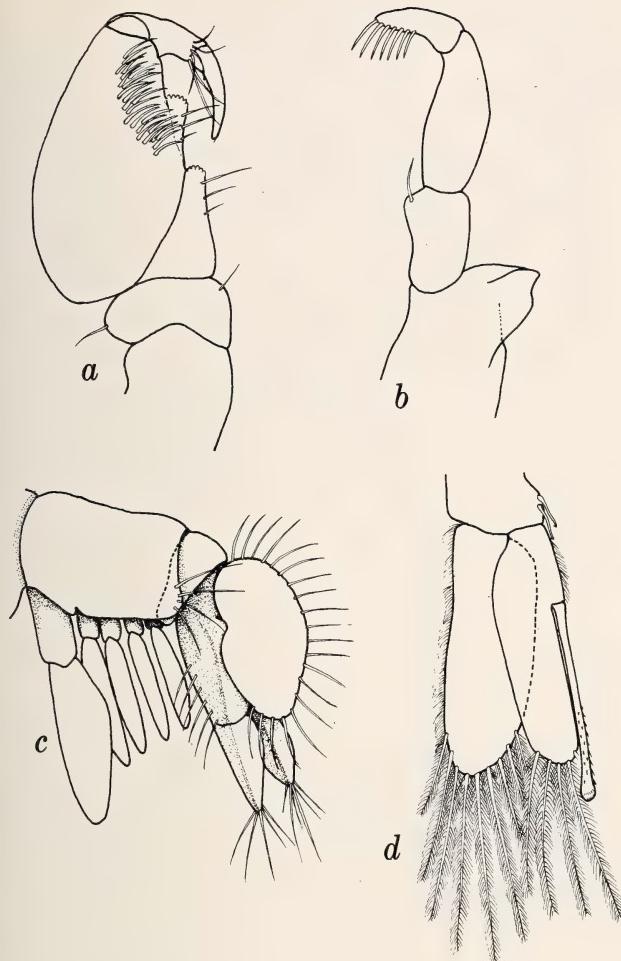


FIGURE 155.—*Mesanthura punctillata* new species, ♂: *a*, pereopod 1; *b*, mandible; *c*, pleon in lateral view; *d*, pleopod 2.

Telson dorsally flattened, distal margin evenly rounded.

Basal antennular peduncle segment broader than, but equal in length to, 2 distal segments; flagellum of 3 articles. Antennal flagellum of 3 articles. Mandibular palp, distal segment with 6 finely serrate spines; incisor with 3 acute cusps; lamina dentata with 5 marginal serrations; molar thumb-like, blunt. Maxilla with 1 strong and 4 slender distal spines. Maxilliped 5-segmented, lacking endite. Pereopod 1 unguis about one-third length of dactylus, propodus broad, palm with hyaline toothed lobe at midlength; carpus triangular, distal rounded part with about 6 serrations. Posterior pereopods with propodus bear-

ing 3 strong posterodistal sensory spines; several spinules on posterior margin; carpus with short anterior margin, underriding propodus, with single sensory spine at anterodistal corner. Pleopod 1 exopod operculiform, 3 times width and subequal in length to endopod, both rami with distal plumose setae; basis with 5 retinaculae. Uropodal exopod ovate, outer margin sinuous, extending slightly beyond distal end of basis, fringed with plumose setae.

**COLOR NOTES.**—Red-brown chromatophores form reticulate pattern on dorsal surface of cephalon, pereon, and pleon. Scattered chromatophores on telson and uropods.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coarse sediment, 24 m.

**Holotype:** ♀ (TL 6.1 mm), Carrie Bow Cay, USNM 171161.

**REMARKS.**—*Mesanthura reticulata* somewhat resembles *M. punctillata* in having scattered chromatophores with a concentration of pigment on the cephalon between the eyes, as well as in the shape of the maxilliped and first pereopod of the female. *Mesanthura punctillata*, however, does not have a notched uropodal exopod, the third mandibular palp segment has 7 more slender spines, rather than the 6 found in *M. reticulata*, and the body proportions of the 2 species also differ. Although only 1 specimen of this species was collected, the pigment pattern is distinctive enough to warrant the formation of a new species.

**ETYMOLOGY.**—The specific name derives from the reticulate dorsal pigment pattern.

### *Minyanthura*, new genus

**DIAGNOSIS.**—Antennular flagellum of 1 article; antennal flagellum of 4 articles. Mandible lacking palp and molar process. Maxilliped 7-segmented, bearing endite. Pleonites 1–5 fused; pleonite 6 fused with telson. Telson with 2 basal statocysts. Pleopod 1, exopod and endopod together forming operculum over branchial chamber. Carpus of pereopods 4–7, rectangular, not underriding propodus.

**TYPE-SPECIES.**—*Minyanthura corallicola*, new species.

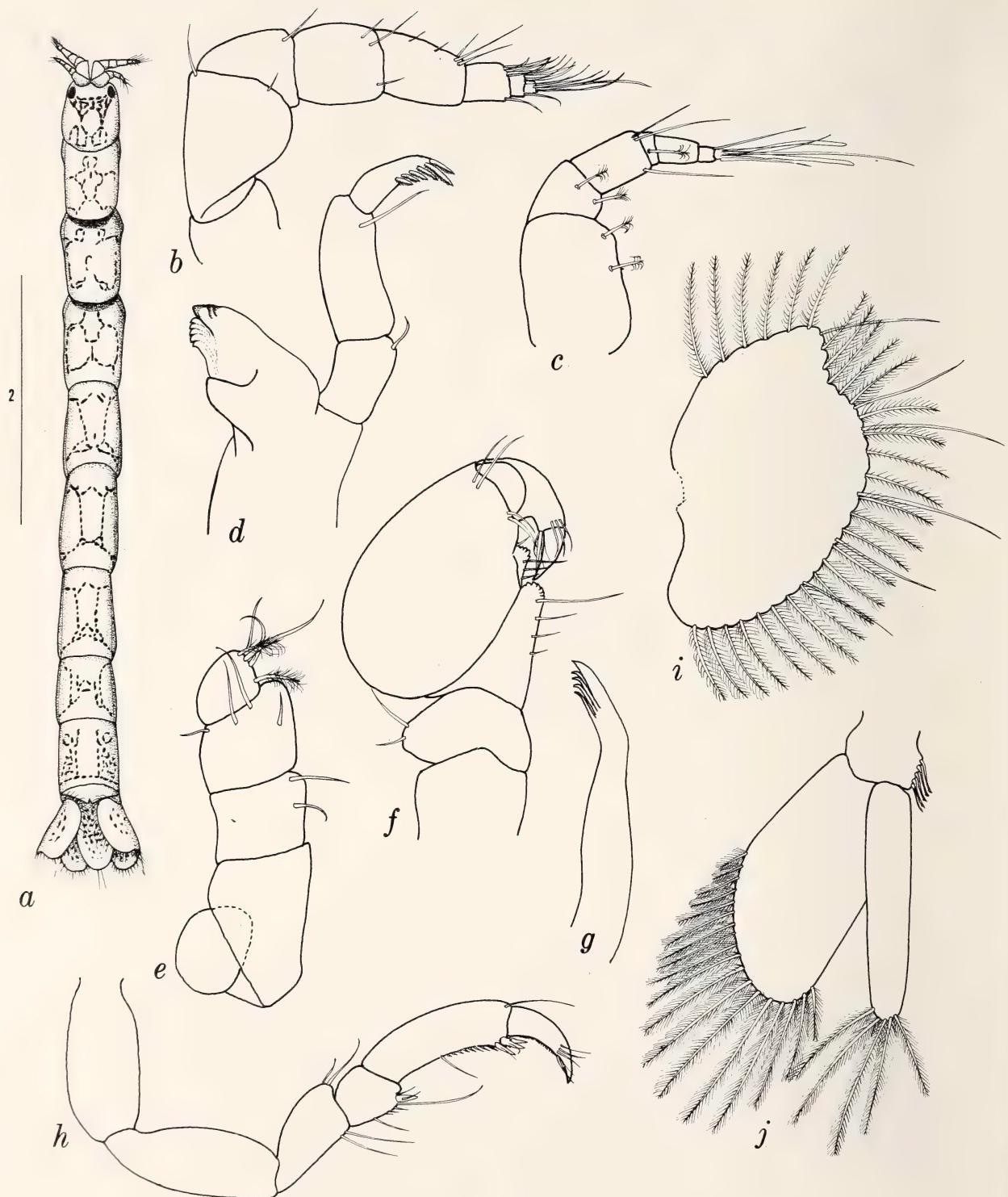


FIGURE 156.—*Mesanthura reticulata* new species, holotype, ♀: *a*, complete specimen; *b*, antenna; *c*, antennifer; *d*, mandible; *e*, maxilliped; *f*, pereopod 1; *g*, maxilla; *h*, pereopod 7; *i*, uropodal exopodite; *j*, pleopod 1.

**ETYMOLOGY.**—The generic name is derived from the Greek *minus* (tiny), and *anthura*, the suffix used for many anthurid genera.

**REMARKS.**—Three anthurid genera, *Belizanthura*, *Ocsanthura*, and *Neohyssura*, possess a 7-segmented maxilliped with an endite. All 3 genera, however, possess nonoperculiform first pleopods and pleonites 1–5 free, and *Ocsanthura* and *Neohyssura* have a short triangular carpus on the posterior 3 pairs of pereopods, which underrides the propodus. The present specimens (assigned herein to *Minyanthura corallicola*), with pleonites 1–5 fused, and pleonite 6 fused with the telson, and operculiform pleopod 1, and a rectangular carpus on the posterior pereopods, obviously cannot be members of any of the above-mentioned genera. Table 25 summarizes these differences.

### *Minyanthura corallicola*, new species

FIGURES 157, 158

**DESCRIPTION OF FEMALE.**—Integument not indurate. Body proportions: C > 1 < 2 < 3 < 4 = 5 > 6 > 7. Cephalon with broadly rounded rostrum extending beyond anterolateral corners; eyes dorsolateral. Pereonite 7 very short. Pleon only slightly longer than pereonite 7; pleonites 1–5 fused, only indicated ventrolaterally; posterior margin of pleonite 5 with row of plumose setae; pleonite 6 fused with telson. Telson broad, distal margin crenulate, broadly rounded or truncate, with few setae; gently convex, longitudinal middorsal ridge present; broad hyaline margin; 2 large basal statocysts.

Antennular peduncle 3-segmented, basal segment as long as rest of appendage, segments 3 and 4 equal in length, and half width of second segment; flagellum reduced to single very short setose article. Antennal peduncle 5-segmented, second segment curved ventrally, subequal in length to segments 3 and 4; flagellum of 4 articles, basal article longer than 3 distal articles together. Mandible with palp represented by single simple seta; incisor of 3 cusps, lamina dentata narrow, with 6 marginal serrations; molar absent. Maxilla with single stout spine and 5 shorter hooked spines. Maxilliped 7-segmented, 5 distal segments together shorter than second segment; thin-

walled endite tipped with single seta, which reaches base of terminal palp segment. Pereopod 1 unguis one-third length of dactylus; propodus with straight unarmed palm, with single stout serrate spine and irregular row of fine combs of setules on inner face. Pereopod 2 similar to pereopod 1. Posterior pereopods propodus with 2 distal serrate spines; ventral margin with row of setule-combs; carpus rectangular, not underriding propodus. Pleopod 1 exopod and endopod lying side by side, subequal in length, together forming operculum over branchial chamber; exopod broadening distally, almost 3 times wider than endopod; both rami with distal plumose setae. Uropodal basis with row of plumose setae on outer margin: exopod widening distally, outer distal angle produced into acutely triangular lobe; inner distal angle rounded and dentate; endopod oval, distal margin serrate, endopod and exopod with broad hyaline border.

**DESCRIPTION OF MALE.**—Body proportions as in female. Eyes larger than in female. Antennular peduncle 3-segmented, flagellum of 2 articles with single terminal aesthetasc. Pereopod 1 as in female. Pleopod 2 endopod with copulatory stylet formed by club-shaped extension of distal end of ramus.

**COLOR NOTES.**—Female, cephalon with broad dark-red-brown band between and posterior to eyes, with lateral unpigmented spots, centrally continuous with pattern on pereonite 1; latter with anterodorsal branching patch; pereonite 2 with dark medio-dorsal ramifying pattern; pereonite 3 with 2 slender lateral bars; pereonite 4 with broad posterodorsal rectangle; pereonite 5 with slender posterodorsal rectangle; tiny wedge between pereonites 6 and 7; pleon with solid middorsal patch with lateral extensions. Male, pigment pattern less defined than in female, with scattered ventral patches.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble, 6–24 m.

*Holotype:* larvigerous ♀ (TL 1.7 mm), Carrie Bow Cay, USNM 171169 (2 larvae in brood pouch, with pigment pattern developed).

*Allotype:* ♂ (TL 1.3 mm), Carrie Bow Cay, USNM 171170.

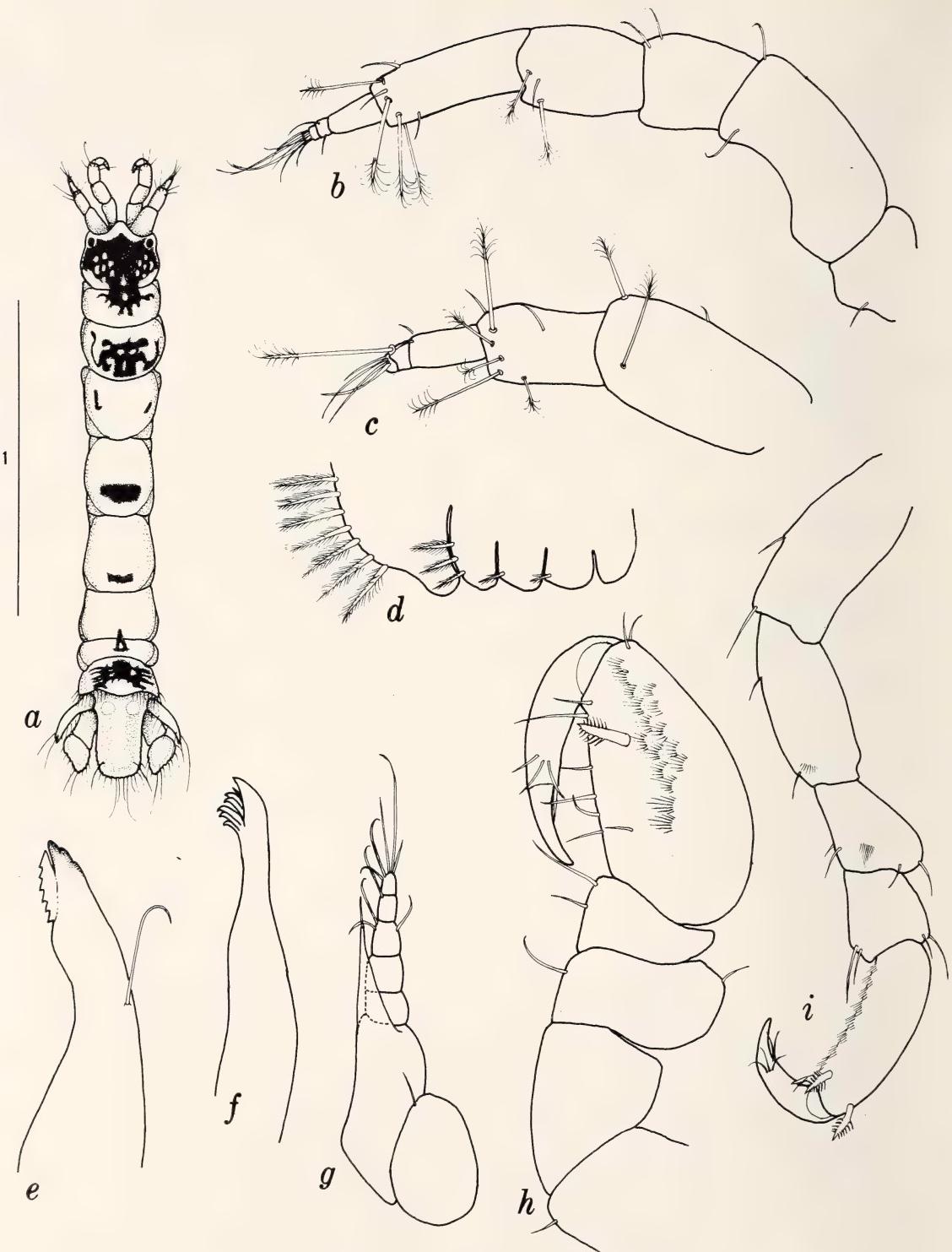


FIGURE 157.—*Minyanthura corallicola* new species, holotype, ♀: *a*, complete specimen; *b*, antenna; *c*, antennule; *d*, lateral margin of anterior pleon; *e*, mandible; *f*, maxilla; *g*, maxilliped; *h*, pereopod 1; *i*, pereopod 6.

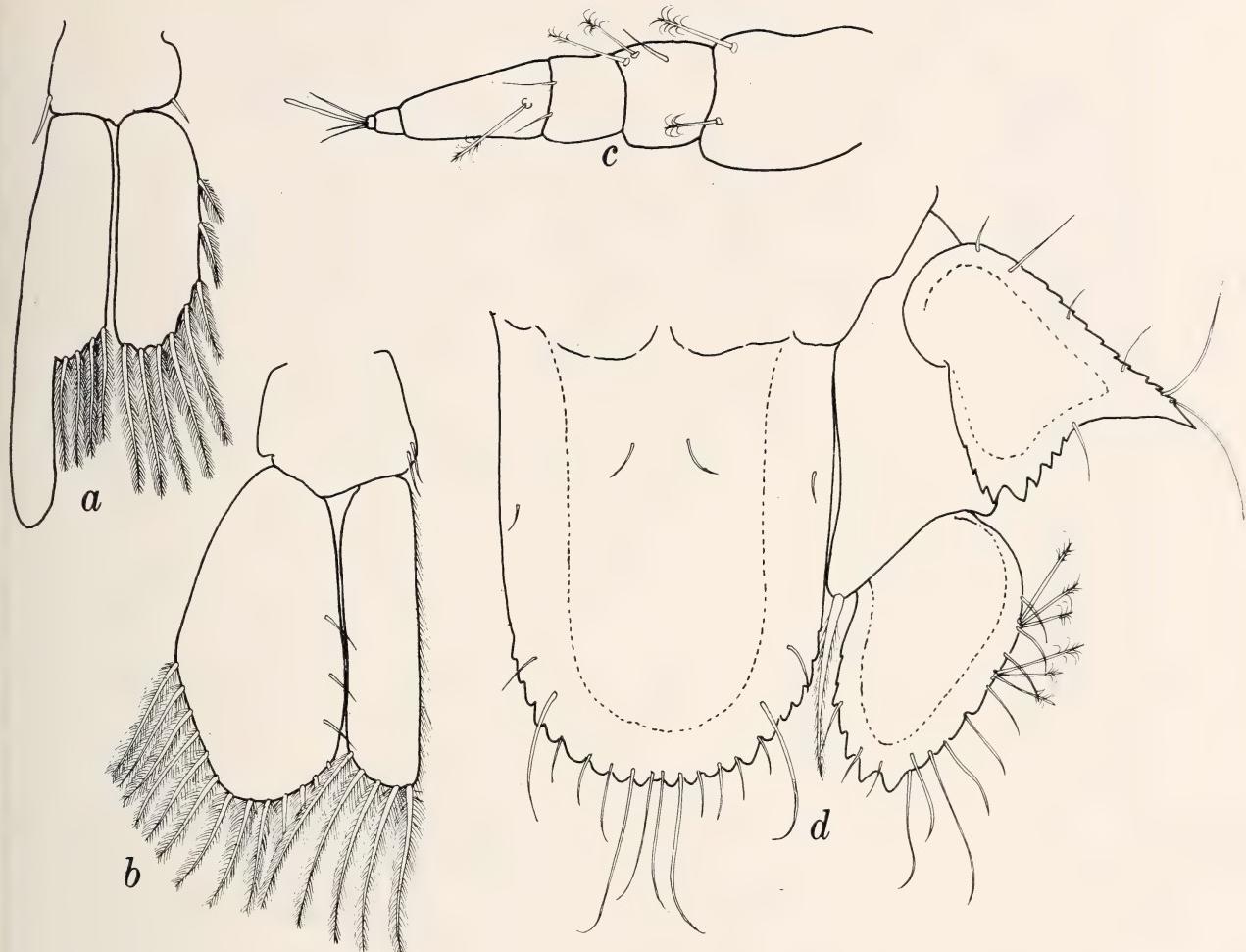


FIGURE 158.—*Minyanthura corallicola* new species, ♂: a, pleopod 2; b, pleopod 1; c, antennule; d, telson and uropod.

*Paratypes*: 4♀ (TL 1.5–1.8 mm), Carrie Bow Cay, USNM 171171.

**ETYMOLOGY**.—The specific name *corallicola*, which means coral-dwelling, is used because all the specimens were removed from coral rubble.

#### *Pendanthura*, Menzies and Glynn

#### *Pendanthura tanaiformis* Menzies and Glynn

FIGURES 159, 160

*Pendanthura tanaiformis* Menzies and Glynn, 1968:32, fig. 12A–I.

**DESCRIPTION OF FEMALE**.—Integument moderately indurate. Cephalon half length of pereonite

1, with rostrum extending beyond anterolateral corners; eyes present in bases of anterolateral lobes. Body proportions: C < 1 > 2 = 3 < 4 = 5 > 6 > 7 > P. Brood pouch formed by 3 pairs oostegites on pereonites 3–5. Pleon very reduced, one-third length of pereonite 7; pleonites indicated only on ventrolateral margins by very short sutures. Telson dorsally flattened, distal margin broadly rounded, pair of statocysts situated at about midlength.

Antennular peduncle 3-segmented, basal segment longest and broadest, distal segment with reduced flagellum of 2 short articles, plus seta-bearing papilla; peduncle armed with large pinnate setae, each articulating on distinct slightly

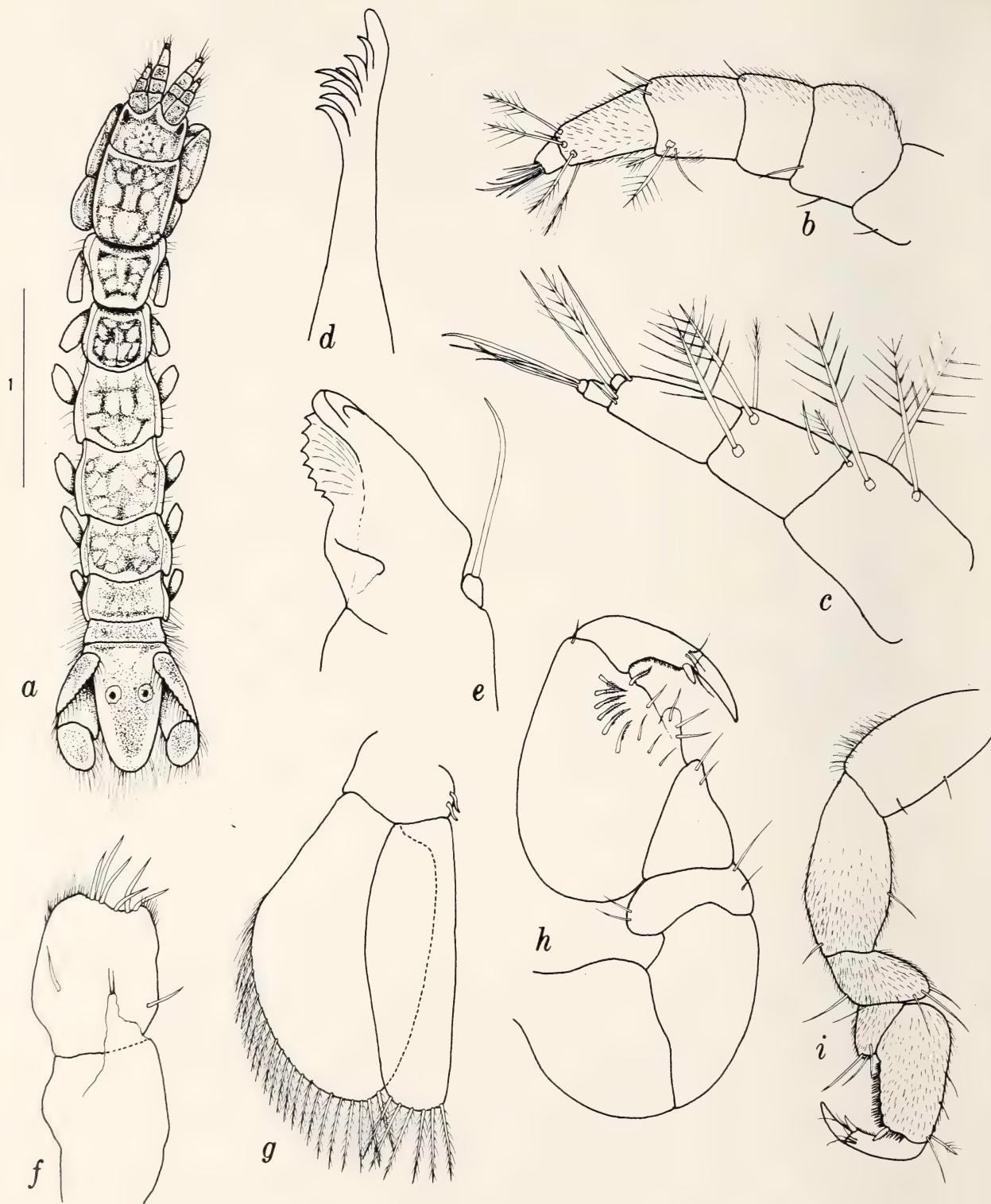


FIGURE 159.—*Pendarthura tanaiformis* Menzies and Glynn, ♀: *a*, complete specimen; *b*, antenna; *c*, antennule; *d*, maxilla; *e*, mandible; *f*, maxilliped; *g*, pleopod 1; *h*, pereopod 1; *i*, pereopod 7.

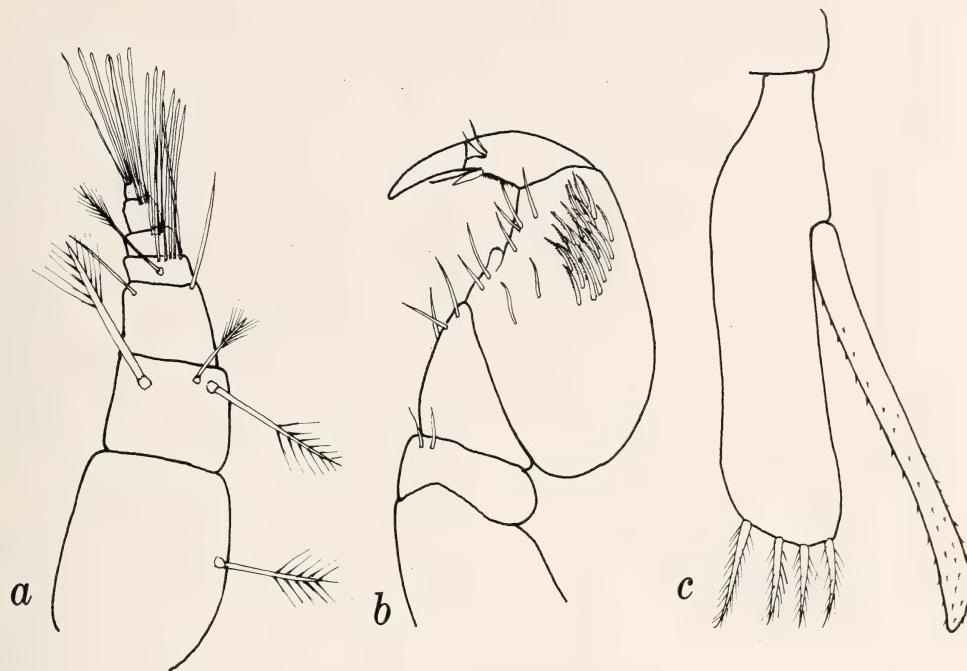


FIGURE 160.—*Pendanthura tanaiformis* Menzies and Glynn, ♂: a, antennule; b, pereopod 1; c, pleopod 2 endopod.

broader base. Antennal peduncle 5-segmented, segments with minute setules; flagellum reduced to single short article. Mandibular palp reduced to small papilla bearing single seta; incisor of 3 rounded, slightly sclerotised cusps; molar reduced; lamina dentata plate with 7 marginal serrations. Maxilla slender, with 8 distal curved spines, terminal spine strongest. Maxilliped 3-segmented, terminal segment with several distal simple setae; thin-walled endite present on inner face, with 2 fine distal setae. Pereopod 1 unguis almost half length of dactylus, ventral margin of latter with fine spinules, strong supplementary spine at base of unguis; propodus with 6 serrate spines on inner face, rounded, very thin transparent lobe on palm with few simple setae. Pereopods 2–7 similar, propodus with posterior margin with crenulations bearing clusters of short spinules and with strong serrate posterodistal spine; carpus short, triangular, underriding propodus; propodus, carpus, merus, and ischium bearing numerous short fine setules. Pleopod 1 exopod operculariform, with numerous laterodistal plumose setae;

endopod half width of exopod, with 6 distal plumose setae; basis with 2 retinaculae. Uropodal exopod distally narrowly rounded, outer (dorsal) margin crenate, with numerous plumose setae, reaching slightly beyond basis; endopod ovoid, bearing plumose and elongate simple setae.

**DESCRIPTION OF MALE.**—Antennular peduncle 3-segmented, flagellum of 4 articles, each with cluster of aesthetascs. Pereopod 1 propodus with dense cluster of curved serrate spines on inner surface, palm with rounded transparent lobe at about midlength. Copulatory stylet of pleopod 2 endopod attached at about proximal third, cylindrical, longer than ramus, apically narrowly rounded, with minute scattered spinules.

**COLOR NOTES.**—Strong reticulate red-brown pigmentation dorsally on cephalon, pereonites, antennae and first pereopods, becoming diffuse on pleon, telson and uropods. The young are released from the brood pouch fully pigmented.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble: 37 ovigerous ♀, 82♀, 45♂, 4 juveniles.

**PREVIOUS RECORDS.**—Puerto Rico.

**REMARKS.**—This is the second record of this unusual genus and species, and the first record of the male. It was thought useful to supplement Menzies and Glynn's description and to figure most of the appendages. A few features require further comment. Menzies and Glynn (1968) described the mandibular palp as being reduced to 2 setae. In fact, the palp may be regarded as 1-segmented, this seta-bearing segment being reduced to a small papilla. Menzies and Glynn mentioned the possible existence of a second flagellar ramus of a single article, on the antennule. More likely, this apparent segment is the slightly enlarged articulated base of one of the large specialized pinnate setae.

## Family PARANTHURIDAE

### *Accalathura*, Barnard

#### *Accalathura crenulata* (Richardson)

*Calathura crenulata* Richardson, 1901:509, figs. 1–4; 1905:74, figs. 58–61.

*Accalathura crenulata*.—Barnard, 1925:147, pl. 4: fig. 18.—Nierstrasz, 1941:242.—Menzies and Glynn, 1968:33, fig. 13A–H.—Schultz, 1969:96, fig. 128.

**MATERIAL EXAMINED.**—Carrie Bow Cay, intertidal to 12 m, sediments, 9♀, 3♂, 9 juveniles; Twin Cays, under mangroves, 1♀.

**PREVIOUS RECORDS.**—Bahamas; Puerto Rico; Yucatan, 40 m; Brazil; Cape Verde Is.

### *Paranthura*, Bate and Westwood

#### *Paranthura caribbiensis*, new species

FIGURES 161, 162

**DESCRIPTION OF FEMALE.**—Integument not indurate, with sparse scattered chromatophores. Cephalon with patch of chromatophores between dorsolateral eyes; tiny, triangular rostrum, not extending beyond anterolateral corners. Body proportions: C < 1 < 2 > 3 < 4 > 5 > 6 > 7. Pleonites 1–5 free, subequal; pleonite 6 with bilobed posterodorsal margin. Telson dorsally flat,

basally constricted, distal margin evenly rounded, with few setae.

Antennular peduncle 3-segmented, basal segment wider than and subequal in length to 2 distal segments; flagellum of 4 articles bearing aesthetascs. Antennal flagellum of single flattened triangular article. Mandibular palp 3-segmented, second segment two and one-half times length of basal segment, third segment with 4 stout fringed spines. Maxilla slender, with 8 distal serrations. Maxilliped 3-segmented, with short endite at base of third segment. Pereopod 1 unguis about one-third length of dactylus; propodus proximally broad, with convex flange and row of 12–14 spines on inner face. Pereopods 2 and 3 similar, subchelate, smaller than pereopod 1; propodal palm armed with 5 sensory spines. Pereopods 4–7 ambulatory, propodus with 2 posterior sensory spines; carpus rectangular, with 2 posterior sensory spines. Pleopod 1 exopod operculiform, four times wider and slightly longer than endopod, both rami with distal plumose setae; basis with 4 retinaculæ. Uropodal endopod subcircular; exopod oval, outer margin slightly sinuous, extending beyond endopod base.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble, shallow sediments, and under mangroves.

**Holotype:** Larvigerous ♀ (TL 4.5 mm), Carrie Bow Cay, USNM 171164 (8 larvae in brood pouch).

**Paratype:** Ovigerous ♀ (TL 4.5 mm), Carrie Bow Cay, USNM 171165.

**Additional Material:** 10♀, 4 juveniles.

**REMARKS.**—This small species of *Paranthura* is easily distinguished from the larger *P. infundibulata*, which also occurs at Carrie Bow Cay, by the serrate and curved telson in the latter species. *Paranthura barnardi* Paul and Menzies, 1971, recorded from Venezuela, is more similar to *P. caribbiensis* in both size and structure. These 2 species can be separated on the uropodal structure (broadly ovate and crenulate in *P. barnardi*, narrowly ovate/sinuous, and entire in *P. caribbiensis*), the telson, which is distally more rounded in *P. caribbiensis*, the presence of a small maxillipedal endite in this species (absent in *P. barnardi*), the

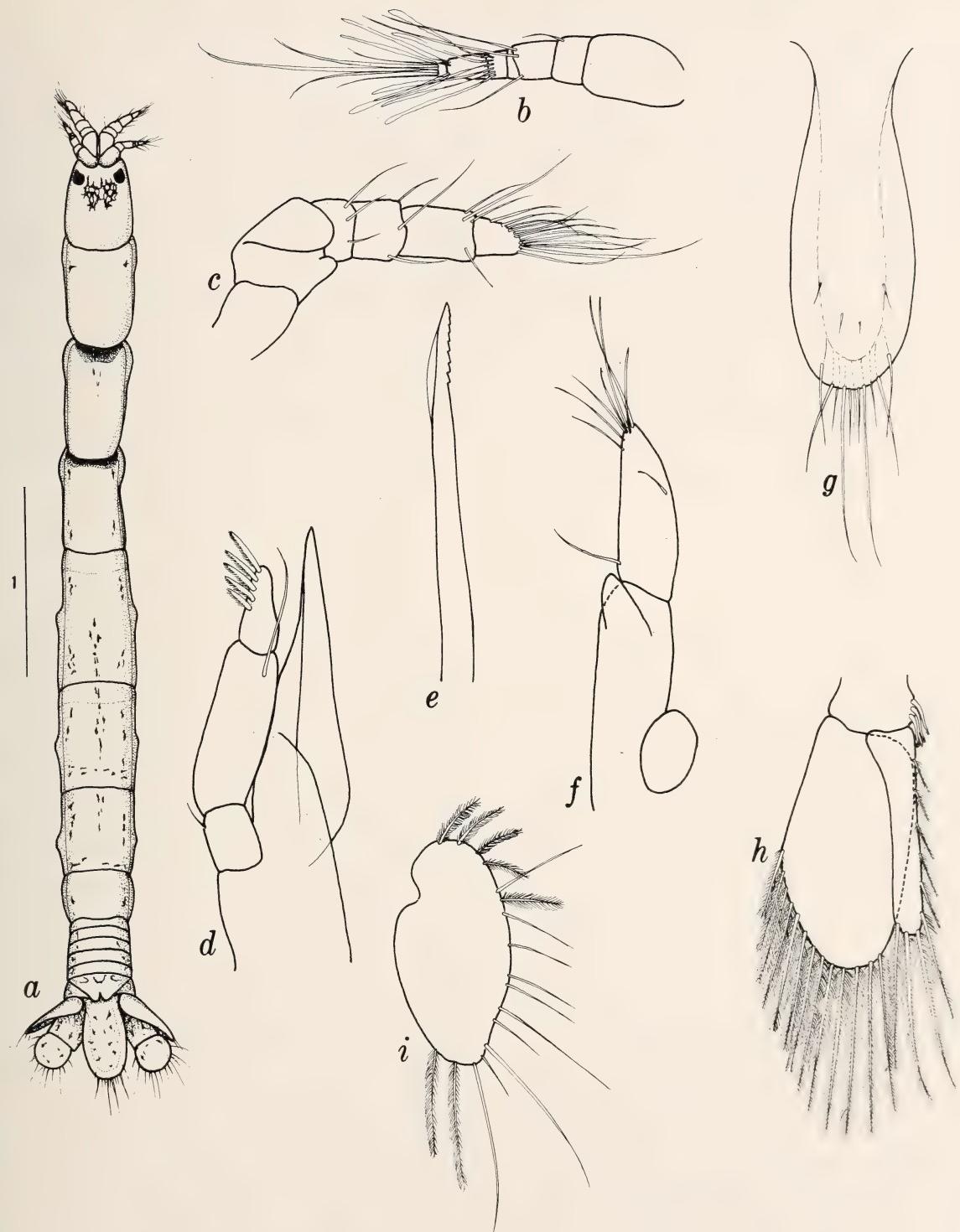


FIGURE 161.—*Paranthura caribiensis* new species, holotype, ♀: *a*, complete specimen; *b*, antennule; *c*, antenna; *d*, mandible; *e*, maxilla; *f*, maxilliped; *g*, telson; *h*, pleopod 1; *i*, uropodal exopod.

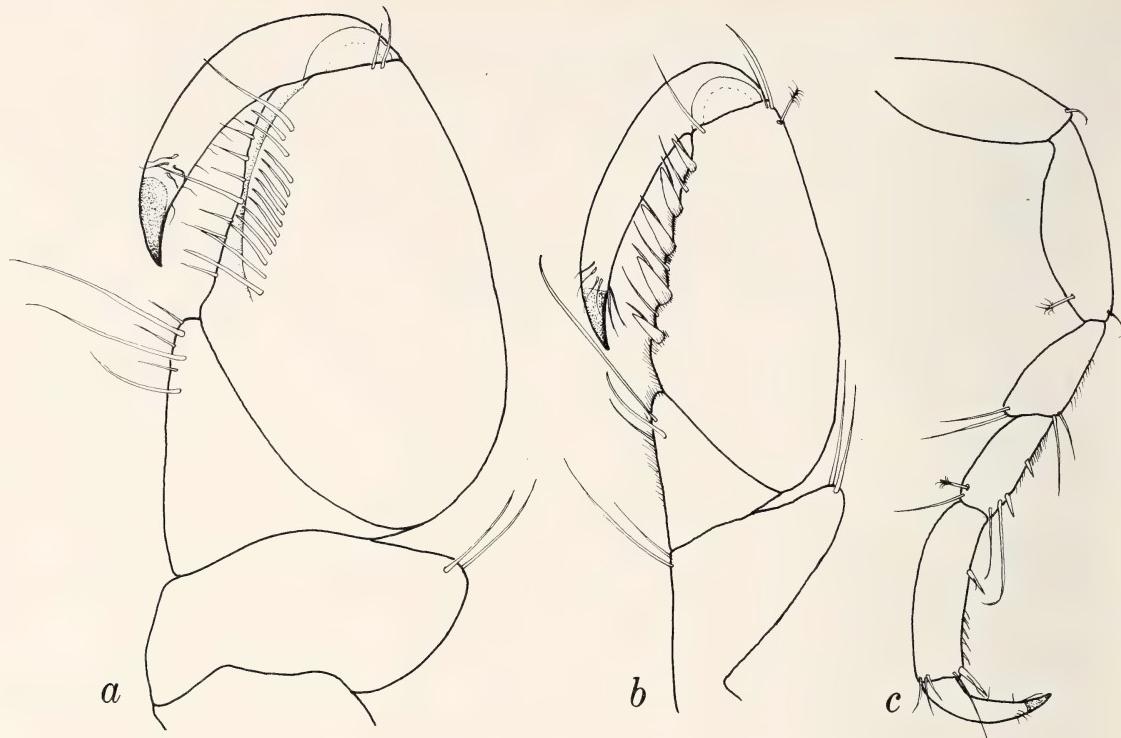


FIGURE 162.—*Paranthura caribbiensis* new species, ♀: a, pereopod 1; b, pereopod 2; c, pereopod 7.

relative proportions of the antennular flagellar articles, and the number of spines on the terminal segment of the mandibular palp (5 in *P. caribbiensis*, 8 in *P. barnardi*). The patch of chromatophores between the eyes in the present species is also a distinctive feature.

**ETYMOLOGY.**—The specific name is derived from the Caribbean Sea in which Carrie Bow Cay is situated.

#### *Paranthura infundibulata* Richardson

*Paranthura infundibulata* Richardson, 1902:284, figs. 15–20; 1905:76, fig. 62.—Barnard, 1925:155.—Menzies and Glynn, 1968:11.—Schultz, 1969:95, fig. 126.—Camp, Whiting, and Martin, 1977:16.

*Paranthura verrillii* Richardson, 1902:286, figs. 21, 22; 1905:77, fig. 63.—Barnard, 1925:155. Menzies and Glynn, 1968:11.

**MATERIAL EXAMINED.**—Carrie Bow Cay, coral rubble: 2♀, 1♂, 12 juveniles.

**PREVIOUS RECORDS.**—Bermuda; Florida.

#### Discussion

**MICROHABITATS.**—The five microhabitats that were sampled for anthuridean isopods in and around Carrie Bow Cay ranged in depth from the intertidal zone to about 24 meters. A general description of the location is presented in Rützler and Macintyre (herein: 9). Although quantitative sampling was not done, about 5 liters of sediment, plant material, and/or rubble was collected at each station, and subjective measures of anthuridean abundance (Table 26) are given in addition to the comments on these microhabitats and their fauna that follow.

1. Coral rubble and algae atop the reef, east side of island. Because much of the reef top is in very shallow water (intertidal to 30 cm) this area is subject to considerable wave action and turbulence under windy or stormy conditions, and to local warming under calm conditions. This environment—with the numerous crevices provided by the Corallinacea-encrusted pieces of coral—shelters a rich population of cryptic ani-

TABLE 26.—Distribution of anthuridean species at Carrie Bow Cay and vicinity by substrate and depth (A = abundant, > 20 specimens; FC = fairly common, 5–19 specimens; P = present, < 5 specimens)

Species	Coral rubble 0–1.5 m	Coarse sediments 0–1.5 m	Algal mat under mangroves 0–1.5 m	Coarse sediments 6–12 m	Coarse sediments 24 m
<i>Accalathura crenulata</i>	—	FC	P	P	—
<i>Apanthura geminsula</i>	A	A	A	—	—
<i>A. signata</i>	P	A	—	—	P
<i>Apanthuroides millae</i>	—	—	—	P	P
<i>Belizanthura imswe</i>	P	P	A	—	—
<i>Mesanthura fasciata</i>	A	A	—	P	P
<i>M. paucidens</i>	FC	A	P	—	—
<i>M. pulchra</i>	FC	P	—	—	—
<i>M. punctillata</i>	FC	P	—	P	—
<i>M. reticulata</i>	—	—	—	—	P
<i>Minyanthura corallicola</i>	—	—	—	P	P
<i>Paranthura caribbiensis</i>	FC	P	P	—	—
<i>P. infundibulata</i>	FC	—	—	—	—
<i>Pendanthura tanaiformis</i>	A	—	—	—	—

mals, including isopods, amphipods, small mollusks, polychaetes, sipunculans, and pycnogonids. Ten species of anthurideans were collected here, several of which also occurred in coarse sediments of weed beds and at the bases of patch corals. *Pendanthura tanaiformis* and *Paranthura infundibulata* were found only in the coral rubble, the former in great numbers. The dark wine-red pigmentation of both species, which live in the tiny holes in the Corallinacea-encrusted coral fragments, probably has a protective function. Probably also connected with this overriding red coloration of the coral rubble is the fact that 8 of the 10 species occurring here have some degree of integumental pigmentation.

2. Coarse white sandy sediments in shallow water. These sediments were taken from *Thalassia* weed beds, *Syringodium* weed beds, or from the sandy patches between patch reefs at a depth of 1.5 m or less. These sites are in protected areas with little wave action, either in the lagoonal area west of the island, or in the shallows between the main reef and the island. Eight species of anthurideans were common to these habitats and to the coral rubble area atop the reef, with *Mesanthura*

*fasciata*, *M. paucidens*, and *Apanthura geminsula* being fairly common to abundant in both habitats.

3. Shallow water sediments and algae at bases of mangroves. This habitat is characterized by calm water in the shade of the mangrove trees, with high accumulations of organic debris, especially mangrove leaves and rootlets, and *Thalassia* leaves. In the several large samples taken under the mangroves, three of the five species of anthurideans collected occurred only rarely, whereas *Belizanthura imswe* and *Apanthura geminsula* were abundant, especially in the dense carpet of *Caulerpa verticillata* J. Agardh growing in less than 15 cm of water between the mangrove trunks and roots. Although *Belizanthura* was taken rarely from other living plants, it is abundant only in the *Caulerpa verticillata*. This algal mat, with its high organic debris content, and with a complex web of fine algal species (including *Cladophora* sp., *Centroceras* sp., *Ceramium* sp., blue-green algae and diatoms), which floats above the *Caulerpa* at high-tide and sinks onto the *Caulerpa* at low-tide, harbors a rich fauna, including many asellote and gnathiid isopods, amphipods, a high diversity of pycnogonids (C. A. Child, pers. comm.), poly-

chaetes, nematodes, cumaceans, leptostracans, and small mollusks, especially the bivalved gastropod *Berthelinia*.

4. Coarse sediments and rubble from the channel between Carrie Bow Cay and South Water Cay. This area is somewhat protected from wave action, but subject to the scouring action of water moving through the channel at a depth of 6 to 12 m. Five species of anthurideans were collected here, none of which appeared to be abundant.

5. Sand trough at base of coral and gorgonian-covered slope. Only two species, *Apanthura signata* and *Mesanthura fasciata* were collected from this area (~24 m depth) and from the intertidal zone. Both were abundant only in the very shallow sediments. Interestingly, *Minyanthura corallicola* resembles *Pendanthura tanaiformis* both in overall size and in having a very short anterior pleonal area. Both species seem to live in crevices in coral rubble, for which a reduction of the body length may be an advantage.

**GENERAL OBSERVATIONS.**—Only male anthurids were taken in the horizontal plankton samples, in shallow water over the reefs suggesting that the

males leave the substrate in search of females. The development of enlarged eyes, filiform aesthetascs of the antennular flagella, and pigmentation over the entire body (rather than confined to the dorsum in female *Mesanthura* spp., for example) are probably adaptations for this reproduction-centered activity. It is unlikely that feeding is a reason for this increased activity, considering the reduction of mouthparts seen in the males of *Belizanthura imswe*, *Apanthura geminsula*, and *Mesanthura punctillata*.

The genus *Mesanthura*, represented here by five species (plus single specimens of two additional species not dealt with in this report) shows very successful radiation into several of the microhabitats mentioned above. Four of these five species co-occur in the coral rubble environments, as well as in the coarse sediments from shallow water. Closer investigation will probably reveal distinctive feeding preferences, and even behavioral differences (considering the distinctive and constant dorsal pigmentation of each species), which would account for this apparent overlap of several species of the same genus.

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# Pycnogonida from Carrie Bow Cay, Belize

C. Allan Child

## ABSTRACT

This is a systematic account of pycnogonids found in the area of Carrie Bow Cay, Belize. Thirty one identified species in 14 genera are discussed of which four are described as new species: *Hedgpethius mammillatus*, *Callipallene belizae*, *Anoplodactylus imswe*, and *Rhynchothorax crenatus*. Most species discussed were found within their previously known range of geographical distribution. Three species are reported for only the second time: *Hedgpethius tridentatus*, previously known from Florida, *Parapallene bermudensis*, from Bermuda, and *Anoplodactylus bahamensis*, from the Bahamas. At Carrie Bow Cay most pycnogonids occur within the littoral depth zone, some extend their range into the sublittoral to a depth of 33 m. Habitats include mangrove roots, algae, and seagrasses, as well as coral and coral rubble.

## Introduction

This is the first report of pycnogonids from the Belizean barrier reef. Only a small collection from the northern portion of this barrier reef in the Territorio de Quintana Roo, Mexico, has been treated in a previous publication (Child, 1979). Previous to that report, the nearest occurrence of pycnogonids reported in the literature were deep water captures of *Anoplodactylus latus* Wilson and *Ascorhynchus serratus* Hedgpeth off Yucatan (Hedgpeth, 1948:226, 259). *Anoplodactylus latus* is also listed from deep water in the Yucatan Channel (Stock, 1975:1055). Other nearby captures are recorded from Cuba to the northeast and from the Caribbean coast of Panama to the south.

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Most published work on pycnogonids centers on descriptive systematics. The small size, cryptic coloration, and very slow movement of these predators make it difficult to record their habits and habitats in the field. Therefore, our knowledge of the ecology of this group is rather poor. Although no attempt was made in this study to observe pycnogonids alive, ecologically relevant information on substrates and associations was obtained and is presented.

All specimens are deposited in the pycnogonid collections of the National Museum of Natural History, Smithsonian Institution, and bear the catalog numbers of the United States National Museum collection (USNM).

**ACKNOWLEDGMENTS.**—My appreciation is extended to the various collectors listed under "material examined" and to P. M. Kier for supporting my 1976 field work in Belize. I am grateful to T. E. Bowman for his critical reading of the manuscript.

## Methods

Pycnogonids were found in a wide variety of microhabitats such as bryozoans, hydroids, and encrusting sponges, algae, or seagrass, and rock rubble covered with one or more of these. Most samples were collected in a depth of less than one meter, some to a maximum depth of 33 m. The gross samples were either examined live under a low-power microscope or preserved before study. Plants and broken-up rock and rubble were agitated in a bucket with dilute formalin in seawater to separate and preserve the microfauna. Floating organisms were then skimmed off and the remainder of the liquid poured through a net to

concentrate the sample. Other suitable substrates such as dock pilings, coral heads, mangrove roots, and rock faces were scraped or chipped into plastic bags for preservation and later examination.

All specimens illustrated in this report were drawn by the author with the aid of a compound microscope and a camera lucida.

### Species List

#### Family AMMOTHEIDAE

- Achelia* Hodge
- Achelia sawayai* Marcus
- Ammothella* Verrill
  - Ammothella appendiculata* (Dohrn)
  - A. exornata* Stock
  - A. marcusii* Hedgpeth
  - A. rugulosa* (Verrill)
- Ascorhynchus* Sars
  - Ascorhynchus latipes* (Cole)
  - Ascorhynchus* sp. cf. *serratus* Hedgpeth
- Eurycyde* Schiödte
  - Eurycyde raphiaster* Loman
- Hedgpethius* Child
  - Hedgpethius mamillatus*, new species
  - H. Tridentatus* Child
- Nymphopsis* Haswell
  - Nymphopsis duodorsospinosa* Hilton
- Tanystylum* Miers
  - Tanystylum birkelandi* Child
  - T. tubirostrum* Stock

#### Family CALLIPALLENIDAE

- Callipallene* Flynn
  - Callipallene belizae*, new species
  - C. emaciata* (Dohrn)
- Parapallene* Carpenter
  - Parapallene bermudensis* Lebour
- Pigromoritus* Calman
  - Pigromoritus timsanus* Calman

#### Family PHOXICHILIDIIDAE

- Anoplodactylus* Wilson
  - Anoplodactylus bahamensis* Child
  - A. batangensis* (Helfer)
  - A. evelinae* Marcus
  - A. imswe*, new species
  - A. jonesii* Child
  - A. maritimus* Hodgson
  - A. monotrema* Stock
  - A. multiclavus* Child
  - A. pectinus* Hedgpeth
  - A. portus* Calman
  - Anoplodactylus* sp.

#### Family ENDEIDAE

- Endeis* Philippi
- Endeis spinosa* (Montagu)

#### Family NYMPHONIDAE

- Nymphon* Fabricius
- Nymphon floridanum* Hedgpeth

#### Family RHYNCHOTHORACIDAE

- Rhyncothorax* Costa
  - Rhyncothorax architectus* Child
  - R. crenatus*, new species

### Family AMMOTHEIDAE

#### *Achelia* Hodge, 1864

#### *Achelia sawayai* Marcus, 1940

*Achelia sawayai*.—Krapp and Kraeuter, 1976:342–343 [literature].—Child, 1979:7–8.

MATERIAL EXAMINED.—Carrie Bow Cay: On corals, 9.1 to 30.5 m, by hand with SCUBA, 7 Apr 1973; 1♂ with eggs. Tidal flats in 0.5 m, coll. K. Rützler, 2 May 1974; 1♀. Tidal flats in 0.5 m, coll. K. Rützler, 4 May 1974; 1♂. Tidal flats in 0–1 m, coll. K. Rützler, 7 May 1974; 1♂. Windward side, reef crest and flat in 0.5 m, 12 Jan 1976; 1 juvenile. Broken rock and rubble at tide line, coll. J. Clark, 17 Jan 1976; 6♂, 1♀, 2 juveniles. Tidal flats, coll. M. Jones, 8 Apr 1976; 1♂. Coral rubble on inner side of reef crest in 0.2–0.4 m, coll. A. Cohen, 15 Jan 1978; 1♀. Rubble at tide line, coll. C. A. Child, 27 Jan 1978; 3 specimens. Rubble at tide line, ocean side, coll. C. A. Child, 28 Jan 1978; 7 specimens. Rocks with algae on reef crest, coll. C. A. Child, 29 Jan 1978; 8 specimens. Algae of the genera *Halimeda* and *Caulerpa* from outer reef crest, coll. C. A. Child, 30 Jan 1978; 9 specimens. From the seagrass *Syringodium* on lagoon flats in 1.3 m, coll. B. Kensley, 1 Feb 1978; 1♀. Ocean side flats, plankton net on bottom in 0.4 m, coll. R. Larson, 30 Jan 1978; 1 juvenile. *Syringodium* bed at S end of lagoon in 1.3 m, coll. B. Kensley, 3 Feb 1978; 6♂, 1 juvenile. Rubble from tide line in 0.3 m, coll. C. A. Child, 4 Feb 1978; 3 specimens. Rubble in front of reef crest in 0.6 m, coll. B. Kensley, 5 Feb 1978; 2♂, 1♀. Carpet of coralline and fine red algae at shore, coll. B. Kensley, 5 Feb 1978; 3♀. From *Halimeda*

in same place; 7 specimens. *Halimeda* and sparse rubble from top of reef ridge, in 18 m, coll. C. A. Child, 7 Feb 1978; 1♀. From other *Halimeda* and rubble nearby, coll. B. Kensley, 7 Feb 1978; 2 specimens.

Tobacco Reef: About 500 m N of South Water Cay, debris at low tide, coll. M. Carpenter and R. Larson, 23 Mar 1977; 2♂.

Twin Cays: N end of dividing channel, on *Halimeda* in 1 m, coll. C. A. Child, 31 Jan 1978; 1♀. NW coast, mat of *Caulerpa verticillata* J. Agardh and mangrove rootlets beneath mangroves, intertidal, coll. C. A. Child, 31 Jan 1978; 3 specimens. NW coast, another *Caulerpa* mat under mangroves, coll. C. A. Child, 2 Feb 1978; 4 specimens. NW coast, mat of *Halimeda* under mangroves, intertidal, coll. C. A. Child, 2 Feb 1978; 4 specimens.

**REMARKS.**—This species is by far the most common pycnogonid in the Carrie Bow area and occurs from the tide line to a depth of 18 meters. It is also common elsewhere in the tropical North and South Atlantic to depths of 65 meters. It has also been found in Madagascar.

**ECOLOGY.**—Several general collections of algae made in the shallow waters of various cays indicate that *Achelia sawayai* lives on associated rubble and other substrates rather than on the algae itself. This species and others were generally not found on clean algae at Carrie Bow Cay, but were common where the algae and rubble were associated with adherent detritus and sessile fauna. Therefore, it is concluded that algae do not provide food for *A. sawayai*, but only a substrate for food attachment.

### ***Ammothella* Verrill, 1900**

#### ***Ammothella appendiculata* (Dohrn, 1881)**

*Ammothella appendiculata*.—Stock, 1955:250–252, fig. 18 [literature]; 1975:973–975.—Child, 1974:497; 1979:9.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Sand trough behind outer reef ridge in 27 m, in coral sand and rubble, coll. C. A. Child, 7 Feb 1978; 2 juveniles. Rubble with *Halimeda* from top of outer

reef ridge in 18 m, coll. B. Kensley, 7 Feb 1978; 1♂ juvenile.

Blue Ground Range (Cays): At S end of northernmost cay, on mangrove roots in 0–1 m, coll. C. A. Child, 30 Apr 1976; 1 juvenile.

Twin Cays: NW coast, from *Rhizophora* roots with algae, sponges, ascidians, and hydroids in 0.5 m, coll. C. A. Child, 31 Jan 1978; 3♂ with eggs, 1♀, 3 juveniles. From *Halimeda* mats along N channel wall in 1 m, coll. C. A. Child, 2 Feb 1978; 3♂ with eggs, 1♂, 7♀, 15 juveniles. From red sponge along wall of N channel in 1.0–1.5 m, coll. M. Carpenter, 2 Feb 1978; 2♂ with eggs.

**REMARKS.**—There is some controversy over the status of this species and *Ammothella rugulosa* (page 358). The wide morphological variation displayed by *A. appendiculata* almost bridges the gap between the two species. Stock (1955:250–252, fig. 18) described two forms of *A. appendiculata*: one with the relatively short appendages of European specimens, and another form with very long appendages from the Caribbean. Stock considered that his two forms reflected differences between the ultimate and penultimate molt in adults, the ultimate molt producing the “long form.” The above material is in agreement with the “long form” but includes several chelate juveniles, thus invalidating the use of adult morphology as an explanation for the range of variation. Raising even more questions than these littoral specimens are the juveniles from depths of 18 and 27 meters with both abdomen and ocular tubercle more than twice as long as the “short form.”

As Stock pointed out, apparently no single visible character can be used to separate *Ammothella appendiculata* from *A. rugulosa* taxonomically, if indeed they are separate species. It is somewhat easier to separate them on the basis of chelifore scape segment lengths (subequal for *A. rugulosa*) and ocular tubercle and abdomen length (measurably shorter for *A. rugulosa*). Stock (1975:973) noted that these differences are probably insufficient to separate the two species. I have no stronger criteria for keeping the species separate, but with the inadequate material currently available, I will regard them as separate until a larger

collection can be measured and diagnosed with more certainty.

**ECOLOGY.**—This species has been found in a wide variety of littoral habitats throughout the Caribbean and on the Pacific side of Panama besides Europe and the Middle East. It has been collected in association with *Rhizophora*, several species of algae, *Thalassia*, sand, rubble, corals, sponges, and ascidians. This distribution indicates a wide food preference, probably including hydroids and other coelenterates, sponges, and possibly ascidians.

### ***Ammothella exornata* Stock, 1975**

*Ammothella exornata* Stock, 1975:975–978, figs. 7c–d, 8.—Child, 1979:9, fig. 3a–c.

**MATERIAL EXAMINED.**—Twin Cays: NW coast, mat of *Caulerpa verticillata* and mangrove rootlets under *Rhizophora* in intertidal, coll. C. A. Child, 2 Feb 1978; 3♀, 2 juveniles.

**REMARKS.**—The male characters were described and figured by Child (1979:9, fig. 3a–c). This is the third record of this species. *Ammothella exornata* is so distinctive that it is easily recognized, even as a juvenile. It is the only known species from the Caribbean littoral having median trunk tubercles.

**ECOLOGY.**—In Belize, this species is known only in association with *Rhizophora mangle* Linnaeus and *Caulerpa* sp. I collected several juveniles associated with algae (not *Caulerpa*) on the prop roots of *R. mangle* in the U.S. Virgin Islands. The type-specimens, from St. Martin, were also collected on and near this mangrove. The only other capture record is Stock's (1975) two specimens collected on algae at Bonaire. The species, however, is not common in this mangrove habitat. At least six algae samples were taken from mangrove roots at about the time of the above capture but no other specimens of *Ammothella exornata* were found. The preferred sessile fauna used for food probably was not with the algae on and around the roots where the six samples were taken. No bryozoans, sponges, or hydroids were found in the *Caulerpa* sample. Therefore, the primary food of

this species, as with most pycnogonid species, remains unknown.

### ***Ammothella marcusii* Hedgpeth, 1948**

*Ammothella marcusii* Hedgpeth, 1948:247–249, fig. 39b–g; 1954:427.—Stock, 1975:975, fig. 7a–b.—Child, 1979:9, 11.

**MATERIAL EXAMINED.**—Carrie Bow Cay: tide flats in 0.5 m, coll. K. Rützler, 4 May 1974; 1♂.

Twin Cays: NW Coast, mat of *Caulerpa verticillata* and mangrove rootlets under *Rhizophora* in intertidal, coll. C. A. Child, 2 Feb 1978; 1♂.

**REMARKS.**—These specimens agree well with Hedgpeth's figures of the type, also a male, and Stock's clarifying figures of the palp and terminal leg segments. Superficially, *Ammothella marcusii* is much more setose than the other species of *Ammothella* in this report. There are many more clubbed, plain, and feathered setae on these specimens than have been figured before.

The species is much less common than its nearest Caribbean relation, *Ammothella appendiculata*, which is known to have an extremely wide range of habitats in its amphi-Atlantic distribution. The above records extend the known range of *A. marcusii* to Belize from Florida, Panama, the eastern Caribbean islands, and the Mexican Pacific coast.

**ECOLOGY.**—This species has been found in shallow water on debris, a sandy reef, *Lithothamnion* flats, rubble, algae, and on tide flats. This distribution shows no pattern except that the principal food of the species is not restricted to particular substrates.

### ***Ammothella rugulosa* (Verrill, 1900)**

*Ammothella rugulosa*.—Stock, 1975:972 [literature].—Child, 1979:11.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Rubble along tide line on ocean side, coll. J. Clark, 17 Jan 1976; 1♂. Large *Halimeda* clump from SE shore, coll. B. Kensley, 5 Feb 1978; 9♂, 2♀.

South Water Cay: SW end, scrapings from dock pilings in 0.5 m, coll. C. A. Child, 30 Jan 1978; 1 juvenile.

Twin Cays: N channel, sponge with ectoprocts in 0.5 m, coll. R. Larson, 31 Jan 1978; 2 juveniles. NW coast, mat of *Caulerpa verticillata* and man-grove rootlets under *Rhizophora* in intertidal, coll. C. A. Child, 31 Jan 1978; 7♂ with eggs, 1♀, 3 juveniles. Another mat from nearby, coll. C. A. Child, 2 Feb 1978; 5♂ with eggs, 2♂, 3♀, 2 juveniles. *Halimeda* mat from nearby, coll. B. Kensley, 2 Feb 1978; 1♀, 1 juvenile. N channel, red sponge from wall of channel in 1.0–1.5 m, coll. M. Carpenter, 2 Feb 1978; 1♂ with eggs.

**REMARKS.**—All specimens of *Ammothella* with short ocular tubercle, short abdomen, and first chelifore segment approximately equal to the second are tentatively placed under *A. rugulosa*. Those without these qualifications are placed with *A. appendiculata* (see remarks under that species).

The female from the *Halimeda* mat of 2 Feb 1978, has an extra eye situated below the normal left anterior eye. It is round, half the size of the one above, and is darkly pigmented, matching the four eyes above.

Scattered records indicate that *Ammothella rugulosa* is distributed from Bermuda to Florida and through the Caribbean to Brazil.

**ECOLOGY.**—This species lives among fouling organisms on ships and piers and has been taken in association with *Sargassum*, in addition to the habitats listed above.

### *Ascorhynchus* Sars, 1877

#### *Ascorhynchus latipes* (Cole, 1906)

*Ascorhynchus latipes*.—Hedgpeth, 1948:256 [literature]; 1954: 427.—Fage, 1952:530.—Stock, 1953:304 [key]; 1954:116; 1975:969.—Child, 1979:15–16.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tide line on ocean side among rocks and rubble, coll. J. Clark, 17 Jan 1976; 1♀, 1 juvenile. Tidal flats on ocean side, from plankton net resting on bottom in 0.5 m at night, coll. R. Larson, 30 Jan 1978; 1♀.

**REMARKS.**—This is another species for which

the range is extended to the western Caribbean. Its occurrence from Florida and the Bahamas to Bonaire, and also at Dakar, Senegal, gives it an amphi-Atlantic distribution.

**ECOLOGY.**—This littoral species appears to have some preference for sand and rock habitats, but the collecting records are too scarce to be certain.

### *Ascorhynchus* sp. cf. *serratum* Hedgpeth, 1948

*Ascorhynchus serratum* Hedgpeth, 1948:259–260, fig. 44a–f.  
*Ascorhynchus serratus*.—Stock, 1975:969.

**MATERIAL EXAMINED.**—Carrie Bow Cay: In coral and algae on outer vertical reef face in 27–30 m, coll. C. A. Child, 29 Apr 1976; 1 juvenile.

**REMARKS.**—This specimen probably represents a new species, but is sufficiently immature that a description should be postponed until an adult can be collected. It shows several similarities to *Ascorhynchus serratum*, in having 3-segmented chelifores, tall ocular and median trunk tubercles, and a long curved oviger claw. The differences exhibited by this juvenile are that it (1) is without lateral process tubercles; (2) has *Ammothella*-like terminal leg segments, but without auxiliary claws; (3) has very short legs and oviger segments in comparison with *A. serratum*; (4) has very short first tibiae; and (5) has very long dorsodistal leg setae. Some or most of these characters may be the result of growth stage, but tubercles are usually well developed by this stage. The absence of lateral process tubercles possibly places this specimen in a separate species.

The depths at which *Ascorhynchus serratum* has been captured, roughly from 400 to 700 meters off Florida and in the Yucatan Channel, would remove this specimen from consideration as the same species except that we know nothing of vertical migration during growth in pycnogonids. We do know that some pycnogonids have a narrow range of temperature tolerances, and perhaps vertical migration is limited by this factor. Certainly, the temperatures from 30 meters to 700 meters cover a wide thermal spectrum.

### *Eurycyde* Schiödte, 1857

#### *Eurycyde raphiaster* Loman, 1912

*Eurycyde raphiaster*.—Stock, 1975:979 [literature].—Child, 1979:21, fig. 5i–j.

MATERIAL EXAMINED.—Carrie Bow Cay: Tidal flats in 0.5 m, coll. K. Rützler, 4 May 1974; 1♂. Rock and algae from both sides of reef crest at low tide, coll. M. Carpenter, 20 Mar 1977; 1♀. Rocks and algae from just in front of reef crest in 0.4 m, coll. B. Kensley, 29 Jan 1978; 1♀. From sandy rubble with *Halimeda* behind outer reef ridge in 27 m, coll. C. A. Child, 7 Feb 1978; 1 juvenile. From *Halimeda* clump behind outer reef ridge in 27 m, coll. B. Kensley, 7 Feb 1978; 1 juvenile.

REMARKS.—Females of this species usually have lateral process and first coxa tubercles that are much smaller than those of the male, and the lateral processes are sometimes placed closer together, imparting a dimorphic appearance to the species. Otherwise, *Eurycyde raphiaster* is easily distinguished from others of the genus in the western Atlantic.

The juveniles collected from 27 meters appear to mark the deepest limit at which this species has been taken in the western Atlantic. Loman (1912:13) lists the capture depth as 91 meters for his type from the Cape Verde Islands.

ECOLOGY.—Three of the above records show this species to be associated with *Halimeda*. It has many other habitats throughout its amphi-Atlantic range. It was one of the few pycnogonids found in the high energy wave action area of the reef crest, but it was also taken in the calm water of the sand trough behind the outer reef ridge.

#### *Hedgpethius* Child, 1974

EMENDED DIAGNOSIS.—Ammotheidae. *Ascorhynchus*-like with minutely papillose body surface, without trunk or lateral process tubercles. Anterior trunk segment longer than combined length of posterior 3 segments; first lateral processes at extreme posterior of first segment, imparting

“long necked” appearance. Proboscis with 3 anterior-pointing tubercles arranged laterally and ventrally around its largest circumference. Scape 2-segmented, very short, chela vestigial. Palp 7- or 8-segmented, third segment with swelling. Female oviger rudimentary, 3-segmented. Male oviger 9-segmented, *Ammothella*-like, without denticulate spines. Propodus with much reduced or missing main claw, auxiliaries large, very curved.

#### *Hedgpethius mamillatus*, new species

FIGURE 163a–f.

MATERIAL EXAMINED.—Carrie Bow Cay: Broken rock and rubble at tide line, coll. J. Clark, 17 Jan 1976; 1 ovigerous female, holotype (USNM 170997).

DESCRIPTION.—First body segment 0.5 longer than combined length of posterior 3 segments. Lateral processes short, less than half trunk diameter, separated by greater than their own diameter, without setae or tubercles. Ocular tubercle a rounded cone as tall as neck diameter, situated at midlength of first trunk segment. Eyes lightly pigmented. Abdomen cylindrical, carried half erect; not extending beyond posterior lateral processes, armed with 2 distal setae.

Proboscis large, ovoid, without marked constrictions, with 2 dorsolateral and 1 ventral anterior-pointing tubercles at widest diameter of proboscis and at one-third its length. Anterior to each tubercle is a slight bulge in same longitudinal axis. Mouth with 3 lateral and ventral slits with flat distinct lips.

Scape 2-segmented, short, carried in cowling around anterior of first trunk segment. First scape segment longest, with single dorsodistal seta. Second segment minute. Chela tiny, with anterior crease and no fingers.

Palp 7-segmented, thin. First 2 segments small, no longer than wide. Third segment about 5 times as long as wide, with a distinct posterior bulge. Fourth and sixth segments tiny, only slightly longer than wide. Fifth segment longest, extremely slender, with 3–4 endal setae. Terminal segment thin, 4 times as long as wide, armed with

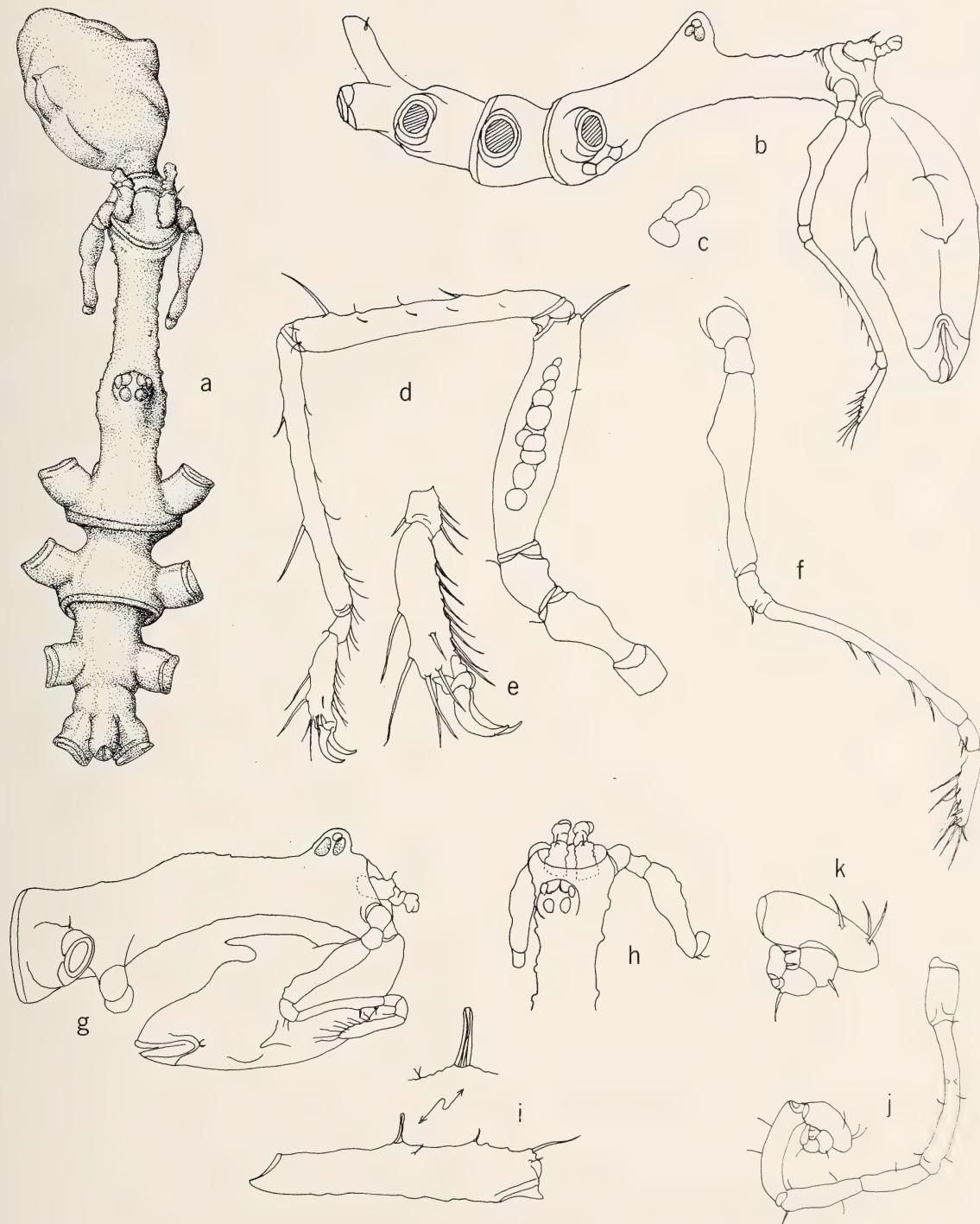


FIGURE 163.—*Hedgpethius mamillatus*, new species (holotype): *a*, trunk; *b*, trunk, lateral; *c*, oviger; *d*, third leg; *e*, terminal segments of third leg; *f*, palp. *Hedgpethius tridentatus* Child, male: *g*, anterior trunk segments, lateral; *h*, anterior of trunk, dorsal; *i*, femur with enlargement of femoral cement gland; *j*, oviger; *k*, oviger terminal segments.

endal and distal setae longer than segment diameter.

Oviger (female) rudimentary, tiny, of 3 segments, arising ventrally just anterior to first lateral processes.

Legs thin, femorae with eggs. Second tibia slightly longer than first, femur slightly shorter than both. Major segments with single long dorsodistal seta, longer than segment diameter, and several short setae. Tarsus and propodus short, without spines but having a row of sole setae as long as segment diameter. Main claw lacking, auxiliaries large, strongly curved.

**MEASUREMENTS (mm).**—Ocular segment length, 0.44; total trunk length (anterior tip to tip of fourth lateral processes), 0.74; trunk width (across second lateral processes), 0.23; proboscis length, 0.37; abdomen length, 0.1; third leg, coxa 1, 0.09, coxa 2, 0.15, coxa 3, 0.09, femur, 0.34, tibia 1, 0.37, tibia 2, 0.38, tarsus, 0.04, propodus, 0.13, auxiliary claw, 0.05.

**DISTRIBUTION.**—Known only from the type-locality, Carrie Bow Cay, Belize, littoral.

**ETYMOLOGY.**—Named for the two breast-like lateral tubercles on the proboscis.

**REMARKS.**—The new species differs from *Hedgpethius tridentatus* in having one less palp segment, a longer abdomen, the ocular tubercle placed on the middle of the neck, and by having large auxiliary claws without a main claw, however small, between them. The male oviger of this new species remains unknown, but will probably resemble that of *H. tridentatus*, with the same extreme sexual dimorphism displayed for that species.

### *Hedgpethius tridentatus* Child, 1974

FIGURE 163g-k.

*Hedgpethius tridentatus* Child, 1974:494–497, fig. 1.

**MATERIAL EXAMINED.**—Twin Cays: NW coast, mat of *Caulerpa verticillata* and mangrove rootlets beneath *Rhizophora* in intertidal, coll. C. A. Child, 31 Jan 1978; 1♂, 1♀. Another mat of the same

substrate from just S of first collection, coll. C. A. Child, 2 Feb 1978; 13 specimens.

**DESCRIPTION OF MALE.**—Proboscis tubercles slightly larger than those of female. Femoral cement gland a tall tube placed at midlength of dorsal surface, perpendicular to femur. Oviger with 9 segments: second the longest; sixth ovoid; terminal 3 segments (strigilis) placed anaxially on middle of sixth segment; strigilis segments short, curved, with simple spines; all but first oviger segment armed with several setae; without terminal claw.

**EMENDED DESCRIPTION OF FEMALE.**—Palp of 8 segments: first two very short; third and fifth longest; sixth and seventh very short; terminal segment thin, with ventral setae. Chelifores of 3 segments, partly hidden by anterior cowling of first trunk segment. Scape with 2 segments, first a short cylinder with dorsodistal seta, second a wrinkled bud, no longer than wide. Chela vestigial, with distal crease but no fingers. Juvenile chela with strongly curved fingers overlapping at tips.

**REMARKS.**—The smallest palp and chelifore segments are extremely difficult to see and were missed in making the first description. The males of this species have the same number of segments in palps and chelifores as listed above in the emended female description.

The extreme sexual dimorphism found in the ovigers of this species is very rare in pycnogonids. In most pycnogonid genera, either ovigers are lacking in the female or the ovigers are smaller slightly modified versions of the male ovigers. Enough females of this genus have now been collected to show that the very reduced ovigers reported in the original description are not misinformation based on damaged specimens, but are the natural state for females of *Hedgpethius*, in which they appear almost embryonic.

This genus was named and published before I received the paper by Turpaeva (1973), in which she assigns a number of species of *Rhopalorhynchus* (Colossendeidae) to a new genus, *Hedgpethia*. According to the International Code of Zoological

Nomenclature, Article 56a, both names must be retained. The two genera are sufficiently different in most characters that they will never become synonymous.

The known distribution for *Hedgpethius tridentatus* is extended from Florida to the Belizean barrier reef islands; all records are littoral.

### *Nymphopsis* Haswell, 1885

#### *Nymphopsis duodorsospinosum* Hilton, 1942a

*Nymphopsis duodorsospinosum* Hilton, 1942a:303–305, pl. 45.—Hedgepeth, 1948:250–252, fig. 40; 1954:427.—Child and Hedgepeth, 1971:609 [list].—Kraeuter, 1973:496.—Stock, 1975:978.—Krapp and Kraeuter, 1976:342.—Child, 1979:21.

MATERIAL EXAMINED.—Carrie Bow Cay: Tidal flats in 0.5 m, coll. K. Rützler, 7 May 1974; 1♀.

REMARKS.—This species is easily recognized by its large size in comparison with tiny littoral species, its legs and trunk, which are crowded with dorsal tubercles, and particularly the two tall trunk tubercles, which separate it from all other pycnogonids known from the Belizean coast. It has been found from the tide line to about 60 meters of depth on various substrates, but its habits and feeding preferences remain unknown.

*Nymphopsis duodorsospinosa* has a wide tropical and temperate distribution, from Georgia and Florida through the Caribbean to Panama and from the Gulf of California to the Pacific coast of Panama. It is also found in the Galapagos Islands.

### *Tanystylum* Miers, 1879

#### *Tanystylum birkelandi* Child, 1979

*Tanystylum birkelandi* Child, 1979:23, fig. 7.

MATERIAL EXAMINED.—Carrie Bow Cay: Flats on ocean side, rubble and calcareous algae from tide line, coll. C. A. Child, 27 Jan 1978; 2♀.

REMARKS.—These two females agree exactly with the female paratype from Galeta Island, on

the Caribbean side of Panama. Since this is only the second capture record for the species, little can be said concerning its habitats, except that it has been taken with coralline and calcareous algae in the littoral. Its distribution is here extended north from Panama to the Belizean coast.

### *Tanystylum tubirostrum* Stock, 1954

*Tanystylum tubirostre* Stock, 1954:117–120, figs. 24–25.—Bourdillon, 1955:600, pl. 3: figs. 2–4.—Child, 1979:34–35.  
*Tanystylum tubirostrum*.—Stock, 1975:984.

MATERIAL EXAMINED.—Twin Cays: NW coast, on roots of *Rhizophora mangle* with adherent red and green sponges, algae, ascidians and hydroids in 0.5 m, coll. C. A. Child, 31 Jan 1978; 2♂, 1♀.

REMARKS.—These specimens agree in all respects with Stock's (1954) description and figures. The present capture extends the known distribution of this species from Bermuda, Puerto Rico, Curaçao and Bonaire, the western Caribbean, and the Pacific shores of Mexico and Panama.

ECOLOGY.—There are few capture records for this species, but these are fairly well documented. It lives in littoral habitats and has been found associated with *Sargassum*, hydroids, and, in this case, with a wealth of potential food. Pycnogonids are known to feed on hydroids and ascidians and because they have been taken in association with sponges, it is assumed that they also feed on the soft parts of sponges.

### Family CALLIPALLENIIDAE

#### *Callipallene* Flynn, 1929

##### *Callipallene belizae*, new species

FIGURE 164.

MATERIAL EXAMINED.—Carrie Bow Cay: *Halimeda* and rubble from outer reef ridge in 18 m, coll. B. Kensley, 7 Feb 1978; 1♂ with eggs, holotype (USNM 171035), 2 juvenile paratypes (USNM 171036). Large clump of *Halimeda* from same area, coll. C. A. Child, 7 Feb 1978; 1♀.

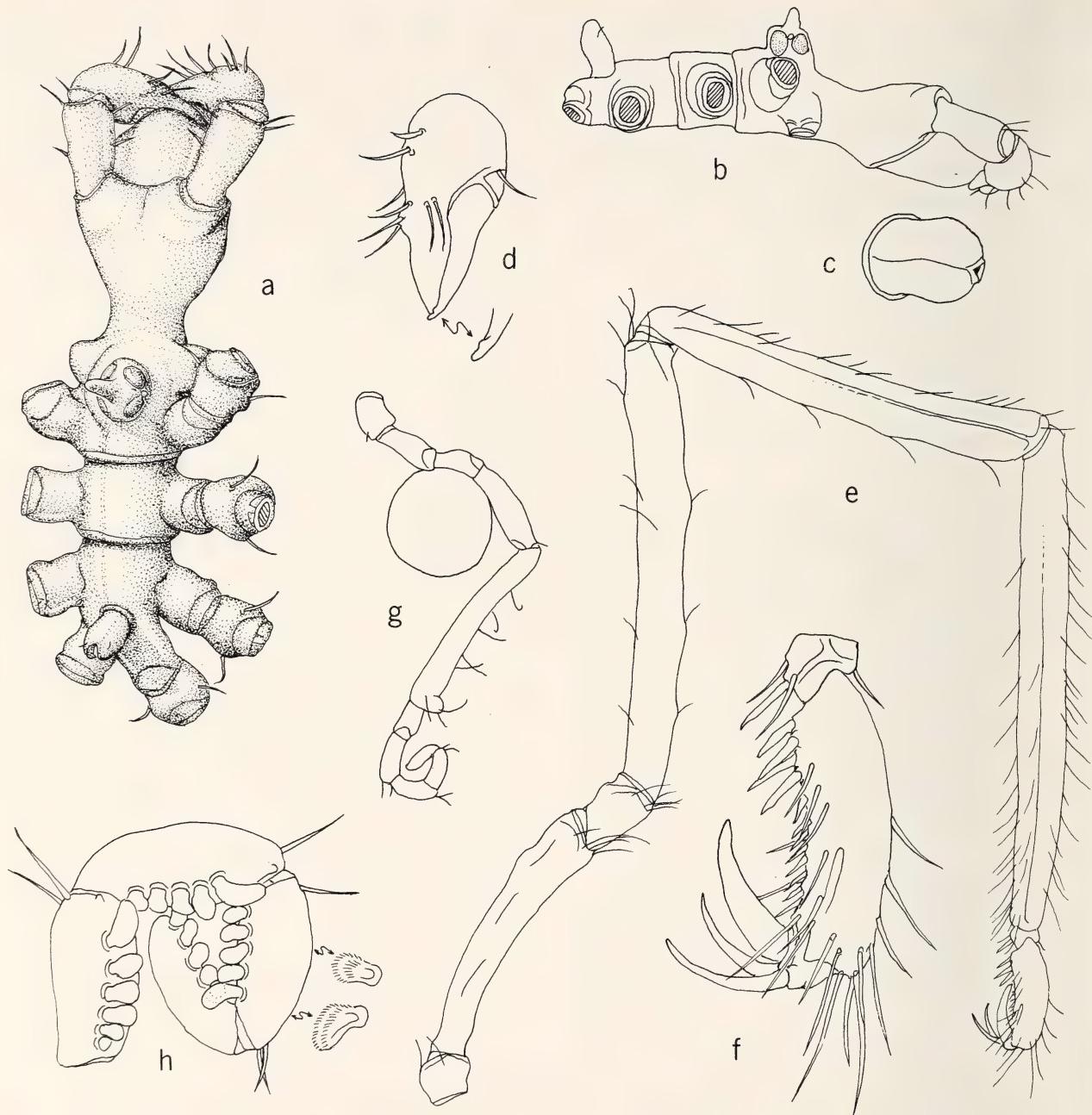


FIGURE 164.—*Callipallene belizae*, new species (holotype): *a*, trunk; *b*, trunk, lateral; *c*, proboscis, ventral; *d*, chela with enlargement of tip of movable finger; *e*, third leg; *f*, terminal segments of third leg; *g*, oviger with single egg; *h*, terminal segments of oviger with enlargement of two spines.

paratype (USNM 171037).

**DESCRIPTION.**—First 2 trunk segment lines present, third lacking. Neck short, unadorned. Lateral processes short, only as long as their diameters, separated by less than their diameters, glabrous. Ocular tubercle a broad truncated cone capped with a thin tubercle as tall as ocular cone. Eyes large, lightly pigmented. Abdomen an irregularly lobed shield.

terminal segments of the third leg. The terminal segments of the oviger with enlargements of two spines.

flated cylinder slightly longer than twice its maximum diameter, armed with 2 distal setae.

Proboscis short, inflated distally and with rounded ventrodistal bulges.

Chelifore scape equal in length to proboscis, armed with lateral and dorsodistal setae. Chela with slightly inflated palm, armed with 7–8 dorsal and 1 ventral setae. Fingers overlap at tips, without setae. Movable finger with single tiny distal tooth, broader than long.

First 3 segments of oviger moderately short, fourth longer, fifth more than twice length of fourth, armed with several setae longer than fifth segment diameter. Distal apophysis of male fifth segment armed with 2 setae. Terminal 4 segments (strigilis) armed with denticulate spines in the formula 6:5:5:5. Denticulate spines dimorphic: proximal spines oval with fine denticulations; distal spine larger, with fan-like projection of denticulations pointing distally on segment.

Legs long, slender, very setose distally. First and third coxae short, little longer than their diameters. Second coxa long, curved, over 5 times longer than its maximum diameter. Femur slightly longer than tibia 1, tibia 2 slightly longer than femur. Cement glands not found. Tarsus short, armed with 2 smooth ventral spines, 1 ventral and 1 dorsal setae. Propodus short, only slightly curved, armed distally and laterally with many long setae. Sole with 4 smooth heel spines and 7 distal spines. Main claw half as long as propodus, auxiliaries about 0.9 times length of main claw, without endal setae or teeth.

**MEASUREMENTS (mm).**—Trunk length (chelifore insertion to tip of fourth lateral processes), 0.89; trunk width (across second lateral processes), 0.37; abdomen length, 0.12; proboscis length, 0.28; third leg, coxa 1, 0.12, coxa 2, 0.65, coxa 3, 0.19, femur, 0.96, tibia 1, 0.77, tibia 2, 1.1, tarsus, 0.06, propodus, 0.28, claw, 0.14.

**DISTRIBUTION.**—Known only from the type-locality, Carrie Bow Cay, Belize, in depths of 18 meters.

**ETYMOLOGY.**—Named for the country where it was discovered, Belize.

**REMARKS.**—This new species resembles Amer-

ican specimens of *Callipallene brevirostris* (Johnston), but has a shorter neck; it is also similar to Caribbean specimens of *C. emaciata*. It differs from both of these species in the following respects: the new species has a tall thin tubercle on top of its truncated ocular cone; it has smooth tarsus and propodus spines whereas the other two have variously crenulated spines; its chela fingers are without teeth except for a single tiny distal tooth on the movable finger; the auxiliary claws are longer than for most American specimens, although those of *C. brevirostris* are sometimes as long; and the posterior trunk segmentation line is lacking, although this is not a reliable taxonomic character with this genus.

Taxonomic distinction among *Callipallene* species is often very difficult to make, not only because several species are very similar, but also because apparently they have more than one adult molt stage with resulting changes in setae, teeth, denticulate spine number and shape, and mensural characters and their ratios. These molt changes add vastly to the difficulty in deciding where variation ends and species begin, a dividing line that will undoubtedly remain uncertain for most *Callipallene* species until large numbers can be compared interspecifically and intraspecifically.

The propodus of *Callipallene belizae* is shorter, less curved, and has many more setae than either *C. brevirostris* or *C. emaciata*. Neither of these species has the very marked dimorphism shown in the denticulate oviger spines of *C. belizae*. The terminal spine on each of the four distal segments is splayed out and canted forward so as to resemble a fan.

**ECOLOGY.**—Since this species has been found only in rubble and *Halimeda* at depths of 18 meters, and the bottom samples from which the species was taken were not preserved for possible food preference organisms, its habits are unknown.

#### *Callipallene emaciata* (Dohrn, 1881)

*Callipallene emaciata emaciata*.—Stock, 1952a:8 [literature].

*Callipallene emaciata*.—Stock, 1975:1011.—Child, 1979:41–42.

MATERIAL EXAMINED.—Carrie Bow Cay: From *Thalassia* bed in 0.5 m, coll. R. Larson, 31 Mar 1977; 1♂ with eggs, 1♂, 2♀, 2 juveniles. From *Dictyota* on reef flat in 0.5 m, coll. R. Larson, 16 Mar 1977; 1 juvenile. Rubble and calcareous algae at wall on ocean side at tide line, coll. C. A. Child, 28 Jan 1978; 1♀. *Syringodium* and sediment from lagoon in 1.5 m, coll. B. Kensley, 1 Feb 1978; 1♀. Plankton sampler on bottom on ocean side flats in 0.5 m, coll. R. Larson, 30 Jan 1978; 1 larva (probably this species).

South Water Cay: Piling scrapings from dock at S end on lagoon side, coll. C. A. Child, 30 Jan 1978; 1 juvenile.

REMARKS.—These are the first records of *Callipallene emaciata* from the western Caribbean. This species has been found in the Mediterranean, Portugal, the Azores, and from Florida and the Caribbean archipelago to the Guianas, primarily in littoral and shallow depths.

ECOLOGY.—This species and two others from the Caribbean coasts, *Callipallene brevirostris* and *C. phantoma* (Dohrn) are generally found associated with fouling organisms on bridge and dock pilings.

### *Parapallene* Carpenter, 1892

#### *Parapallene bermudensis* Lebour, 1949

FIGURE 165.

*Parapallene bermudensis* Lebour, 1949:930–932, figs. 2–3.

MATERIAL EXAMINED.—Carrie Bow Cay: Coral, sand and rubble from sand trough behind outer reef ridge at 27 m, coll. C. A. Child, 6 Feb 1978; 1♀ subadult. Sand and rubble from slightly S of above sample in 27 m, coll. C. A. Child, 7 Feb 1978; 1♂ juvenile.

REMARKS.—Although neither of these specimens is fully mature, they agree with Lebour's (1949) description and represent only the second record of this species; the type-locality is Bermuda. An unreported female from about the same depth in the Bahama Islands is in the collections of the National Museum of Natural History.

Since Lebour's (1949) figures are somewhat stylized and several details are omitted from her drawings and description, I have prepared a set of figures of the male for clarification. Lebour stated that the chela fingers lack denticulations, but both the Bahama specimen and the above two have very small denticulations or teeth on one or both fingers of the chela.

The species has raised lips and an oral fringe of tiny setae. The propodus has two major heel spines unlike the figure and description of Lebour's (1949:931–932, figs. 3–7) specimen. The ventrodistal second tibia spine, major tarsal spine, and the sole spines all show a slight serration on their inner surfaces. The auxiliary claws are slightly shorter than those figured by Lebour.

The ovigers of the Carrie Bow female are shorter than those of the type-specimen, but the female was about to molt and the next (adult) stage oviger can be seen clearly within the outer chitinous layer. The oviger of the Carrie Bow male is still the unsegmented curled appendage of a juvenile.

A distinctive character of this species is its spination. There are short broad spines on the first coxae and a series of these spines around the insertion of the chelifores and proboscis. The spines have an annulated hollow interior without the annulations being carried through to the outer surface (Figure 165f). Elsewhere on the animal, where other typical spines and setae are present, these annulated spines are absent.

The Carrie Bow specimens represent a range extension to the western Caribbean for this species.

ECOLOGY.—The four available records for this species indicate that it has a very restricted depth preference. All four specimens reportedly have been taken in depths of 27 to 33 meters (90 to 100 ft). Lebour's (1949) type was taken "with fragments of hydroids and weeds." The Carrie Bow specimens were taken from rubble with some algae and probably a number of hydroids, although none of the latter were saved. No habitat data are available on the Bahamas specimen.

The Carrie Bow specimens were light brownish green. Pigmentation and feeding preference have

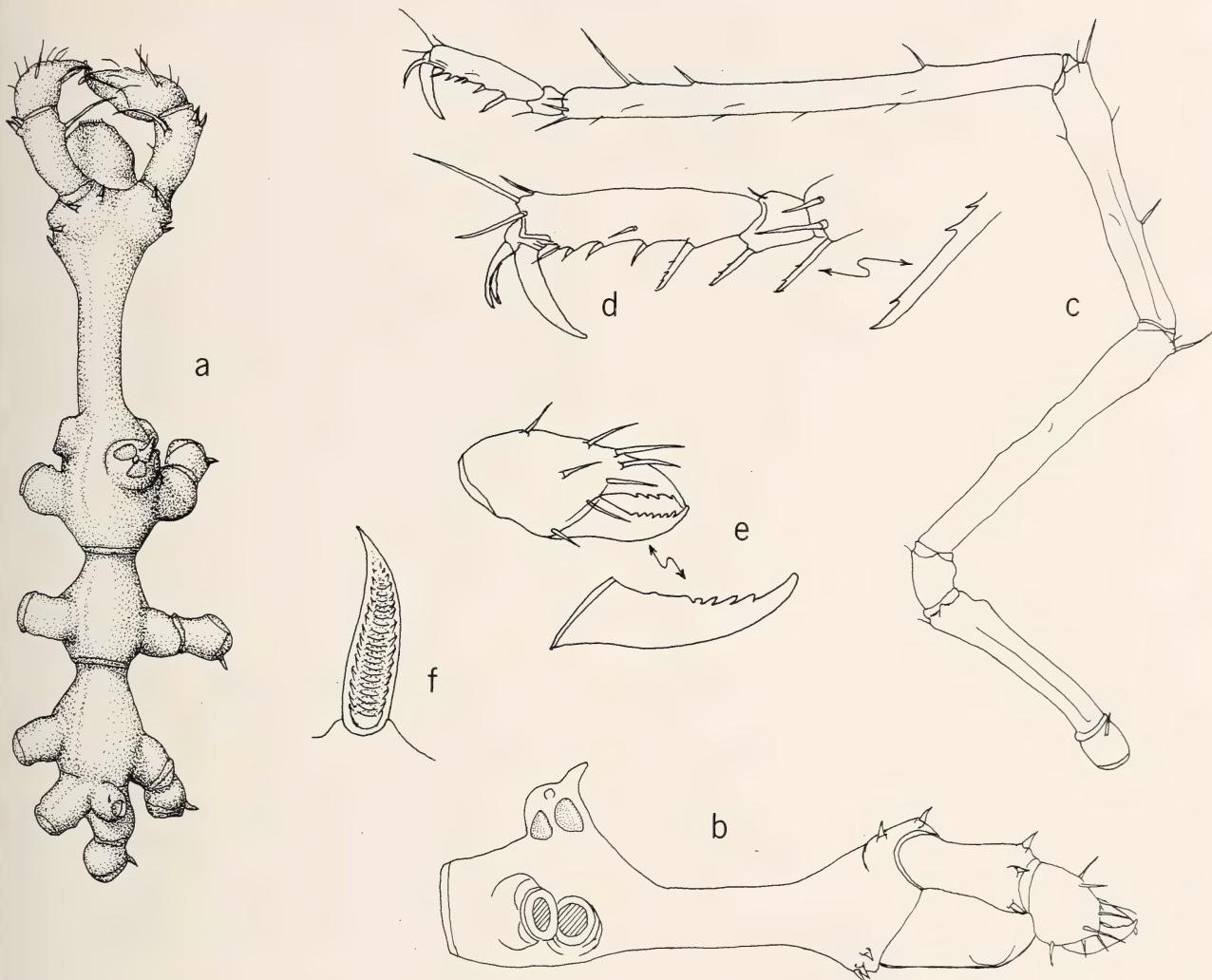


FIGURE 165.—*Parapallene bermudensis* Lebour, juvenile male: *a*, trunk; *b*, anterior trunk segments, lateral; *c*, third leg; *d*, terminal segments of third leg with enlargement of spine; *e*, chela with enlargement of movable finger; *f*, annulated spine.

not been correlated, but most literature references concerning live pycnogonids state that generally they are colored the same as the substrate making them difficult to see. Their color probably represents some of the algal substrate on which many pycnogonids find their food source.

#### *Pigromitus* Calman, 1927

#### *Pigromitus timsanus* Calman, 1927

*Pigromitus timsanus* Calman, 1927:408–410, fig. 104a–f.—Hedgpeth, 1947:7 [text]; 1948:214–216, fig. 23.—Stock,

1968a:46; 1975:1015–1016.—Lipkin and Safriel, 1971: 9.—Arnaud, 1972:159–160.—Child, 1979:46, 47.  
*Clotenops prima* Hilton, 1942b:52–53, fig. 8.

MATERIAL EXAMINED.—Carrie Bow Cay: Among rocks and rubble on ocean side at tide line, coll. J. Clark, 17 Jan 1976; 2 juveniles.

Twin Cays: Among *Rhizophora* roots along N edge of dividing channel at S end of Cays in 0.6 m, coll. C. A. Child, 25 Apr 1976; 1♂ with eggs.

REMARKS.—This species has a pantropical distribution. This is the second record of capture in the western and southwestern Caribbean, the first being from the Caribbean coast of Panama.

**ECOLOGY.**—The many and varied habitats of this species include corals, algae, zoanthids, mangroves, rubble, and molluscan cavities. It was also found among unspecified fouling organisms on pilings, almost always at intertidal and subtidal depths.

### Family PHOXICHILIDIIDAE

#### *Anoplodactylus* Wilson, 1878

##### *Anoplodactylus bahamensis* Child, 1977

*Anoplodactylus bahamensis* Child, 1977:587–589, fig. 2.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats in 0.5 m, coll. K. Rützler, 2 May 1974; 1♂.

**REMARKS.**—This species was originally described (Child, 1977:587) as having teeth only on the movable fingers of the chelae. The male collected here has 3 tiny low teeth on the immovable finger also, but it is otherwise indistinguishable from the type, also a male.

This Carrie Bow male extends the known distribution to the western Caribbean.

The habitats or associations of this species remain unknown. It has been found at depths of 0.5 and 12 meters.

##### *Anoplodactylus batangensis* (Helper, 1938)

*Pycnosoma batangense* Helper, 1938:174–176, fig. 6a–c.

*Anoplodactylus batangensis*.—Stock, 1968a:54 [literature]; 1975: 1082–1083, fig. 43c–d.—Arnaud, 1973:957, figs. 3–4.—Child, 1979:50.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats at tide line, coll. K. Rützler, 23 Apr 1974; 1♂ with eggs, 1♀. Tidal flats at 0.5 m, coll. K. Rützler, 2 May 1974; 1♂. From *Dictyota* on reef flat in 0.5 m, coll. R. Larson, 16 Mar 1977; 1♂ juvenile. From *Thalassia* bed in 0.5 m, coll. R. Larson, 31 Mar 1977; 1 juvenile. Rubble and *Halimeda* from outer reef crest in 0.5 m, coll. B. Kensley, 30 Jan 1978; 1♂ with eggs. Mixed carpet of red algae and compact corallines at SE end shore, coll. B. Kensley, 5 Apr 1978; 1♂.

South Water Cay: *Thalassia* and red sponge

beyond dock at S end in 1 m, coll. B. Kensley, 30 Jan 1978; 3♀.

Twin Cays: NW coast, mat of *Caulerpa verticillata* and mangrove rootlets from under *Rhizophora*, intertidal, coll. C. A. Child, 31 Jan 1978; 1♂, several juveniles. Another *C. verticillata* and rootlet mat from nearby, coll. C. A. Child, 2 Feb 1978; 3♂. A mat of *Halimeda* from nearby, coll. B. Kensley, 2 Feb 1978; 1♀.

**REMARKS.**—This species is easily recognized by its anteriorly curved and tapered proboscis, unique among the many species of this genus.

Several live and even freshly killed specimens, particularly the 3♂ found on *Caulerpa*, 2 Feb 1978, had a broad chalk-white stripe running from the posterior of the ocular tubercle to the base of the abdomen. The remainder of these animals ranged from cream to slightly straw colored, except for a chalk-white band around each distal leg segment suture. This white color was not associated with the intestinal diverticula, which could be seen below and separate from the color line.

**ECOLOGY.**—Stock (1975:1083) mentioned that males seem to be rare, but both in this collection and in another from Panama, males appear in equal or greater numbers than females. Of the 14 adults in this collection, there are 9 males and 5 females; 2 of the males bear eggs. This imbalance may be related to collecting methods. Pycnogonids are generally found incidentally by sorters who are looking for other organisms and therefore many are missed.

The habitats of this species are quite varied, and include algae, *Thalassia*, sponges, rubble, and *Rhizophora*. All specimens were taken in littoral depths and most records in the literature are also from shallow water.

##### *Anoplodactylus evelinae* Marcus, 1940

*Anoplodactylus evelinae* Marcus, 1940:55–58, pl. 4.—Hedgpeth, 1948:232, fig. 31.—Child, 1979: 53.

*Anoplodactylus* (*Labidodactylus*) *evelinae*.—Stock, 1954:128; 1975:1083.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats at tide line, coll. K. Rützler, 23 Apr 1974;

1♂. *Thalassia* bed in 0.5 m, coll. R. Larson, 31 Mar 1977; 1♂ with eggs. Rubble and calcareous algae on ocean side in 0.3 m, coll. C. A. Child, 27 Jan 1978; 1♀. *Halimeda*, *Caulerpa*, and rubble from outer reef crest in 0.5 m, coll. B. Kensley, 30 Jan 1978; 1♀. Clump of *Halimeda* at shore, SE end, coll. B. Kensley, 5 Feb 1978; 1♀.

Twin Cays: NW coast, *Rhizophora* roots with algae, hydroids, ascidians, and bryozoans in 0.5 m, coll. C. A. Child, 31 Jan 1978; 2 juveniles. NW coast, mat of *Caulerpa verticillata* and mangrove rootlets under *Rhizophora*, intertidal, coll. C. A. Child, 2 Feb 1978; 4♂, 2♀. Mat of *Halimeda* from same area, coll. B. Kensley, 2 Feb 1978; 1♀.

**REMARKS.**—This is another easily recognized species. It is very "stumpy" in appearance, with a short and broad ocular tubercle, abdomen, and proboscis. The legs are robust and the very pointed heel with its short spine makes a reliable recognition character.

It is common in the western Caribbean. The above collections produced 14 specimens from the littoral.

**ECOLOGY.**—The habits of *Anoplodactylus evelinae* are unknown, but it is found together with other species of pycnogonids in algae, *Thalassia*, *Rhizophora*, rubble, and among sessile animals. The Belizean collections do not support Stock's (1975: 1083) suggestion that this species is a sand burrower.

### *Anoplodactylus imswe*, new species

FIGURE 166

**MATERIAL EXAMINED.**—Tobacco Reef: Reef top about 500 m N of South Water Cay, intertidal, coll. M. Carpenter and R. Larson, 23 Mar 1977; 1♂ holotype (USNM 171122).

Carrie Bow Cay: Tidal flats in 0.5 m, coll. K. Rützler, 4 May 1974; 1♀ paratype (USNM 171123). Tidal flats in 0.5 m, coll. K. Rützler, 7 May 1974; 1♀ paratype (USNM 171124).

**DESCRIPTION.**—Trunk with first two intersegmental lines well marked, third incomplete, marked only by slight depression dorsally. Lateral processes separated by slightly less than their

diameters, each as long as trunk diameter, without tubercles, armed with 1–3 dorsodistal setae. Ocular tubercle a moderately tall cylinder twice as tall as its diameter, capped by triangular cone. Eyes distally on cylinder, darkly pigmented. Neck armed with single seta lateral to, and in front of, ocular tubercle. Abdomen almost 3 times its diameter, bent erect, armed with several distal setae.

Chelifores thin, scape armed with several distal setae. Chela ovoid, fingers shorter than palm, well curved at tips, without teeth. Palm with several distal setae; movable finger with 3 ectal setae.

Oviger with robust curved basal segment. Second segment only slightly longer, cylindrical, armed with ectal row of 6–7 short setae. Third segment longest, slightly less than half again as long as second segment, armed with several ectal and endal setae. Terminal 3 segments each shorter than last, moderately setose distally with distal setae longer than segment diameter. Terminal segment thin, pointed at tip.

Leg with first coxae armed with 2–4 dorsodistal setae, without tubercles. Second coxae of third and fourth legs with ventrodistal genital spur almost as long as segment diameter, carrying genital orifice at tip. Coxae of first and second legs without spurs or orifices. Third coxae armed with several distal setae. Femur the longest leg segment with first tibia longer than second, each armed with several short setae and a single long dorsodistal seta, as long or longer than segment diameter. Seta of femur mounted on short tubercle. Femoral cement gland a long, thin, flask-shaped tube, canted distally, situated at less than one-third length of femur. Tarsus roughly triangular, with several ventral setae. Propodus stout; heel perpendicular, armed with single large spine and 5 smaller spines. Sole armed with 6–7 curved spines and several lateral setae; distal lamina one-fifth sole length. Claw robust, strongly curved. Auxiliary claws lacking.

**MEASUREMENTS (mm).**—Trunk length (chelifore insertion to tip of fourth lateral processes), 0.93; trunk width (across first lateral processes), 0.63; proboscis length, 0.52; abdomen length,

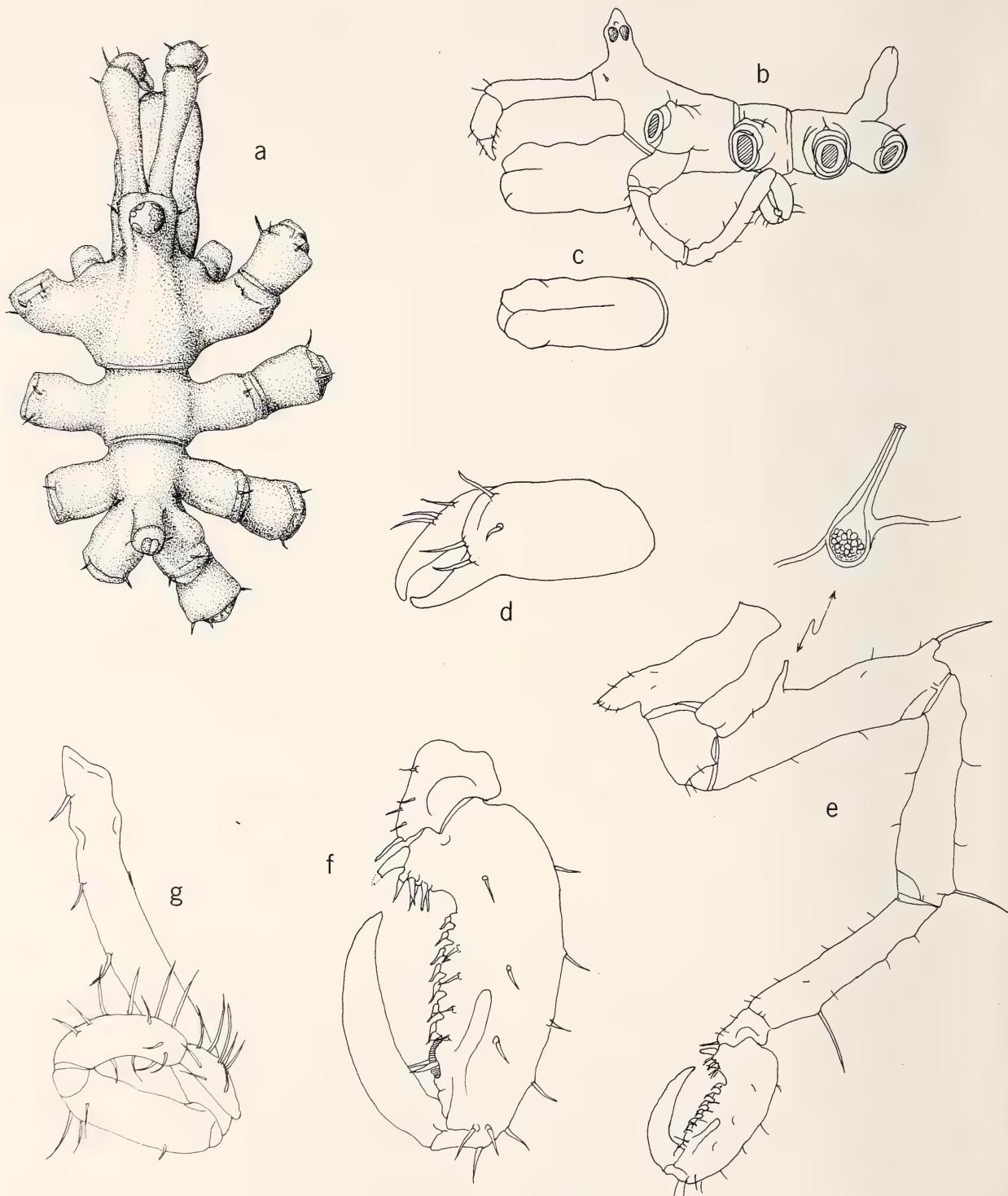


FIGURE 166—*Anoplodactylus imswe*, new species (holotype): *a*, trunk; *b*, trunk, lateral; *c*, proboscis, ventral; *d*, chela; *e*, third leg with enlargement of femoral cement gland; *f*, terminal segments of third leg; *g*, oviger terminal segments.

0.24; third leg, coxa 1, 0.21, coxa 2, 0.42, coxa 3, 0.2, femur, 0.55, tibia 1, 0.52, tibia 2, 0.47, tarsus, 0.09, propodus, 0.34, claw, 0.23.

**DISTRIBUTION.**—Known only from the type-locality, the Belizean barrier reef at Tobacco Reef and Carrie Bow Cay at a depth of 0.5 meters.

**ETYMOLOGY.**—This species is named for the Smithsonian Institution Investigations of Marine Shallow-Water Ecosystems (IMSWE) Project.

**REMARKS.**—The femoral cement glands of this species are not unique among species of *Anoplodactylus*. They are almost exactly like the glands of *A. batangensis*, but they are placed slightly farther back toward the proximal end of the segment in the new species. Other differences in *A. imswe* remove it from consideration as *A. batangensis*. Most notably, the proboscis in the new species is cylindrical whereas in *A. batangensis* it is constricted distally to a thin tube. The new species also has longer first oviger segments, longer and less setose leg segments, longer ocular tubercle and abdomen, and lacks low lateral process tubercles. The propodus, however, with its heel and heel spine, sole spines, and lack of auxiliaries, is strikingly similar in both species.

This species is similar to *Anoplodactylus erectus* Cole in the shape of the trunk, ocular tubercle, oviger, and abdomen, but the propodus characters and the cement glands are very different. It is also similar to *A. maritimus*. In comparison with Giltay's male type specimen of *A. parvus* (= *A. maritimus*, fide Stock, 1975:1069–1074), the ovigers, chelifores, trunk, and propodus shape of *A. imswe* are very close to those of the type of *A. parvus*. The differences are (1) the propodus of *A. parvus* has two heel spines and auxiliary claws, (2) the abdomen and ocular tubercle are shorter, (3) there are no discernible trunk segmentation lines, and (4) the cement glands are tiny short tubes where they emerge from the femora.

**ECOLOGY.**—The three specimens from Belize, although collected in separate locations, all share a distinct color pattern. When freshly killed, the Tobacco Reef specimen had a bright purple gut. After storage in alcohol for a year or more, all three specimens have deep blue intestinal tracts.

This blue pigment appears to be a reliable recognition character for this species, at least on the Belizean barrier reef. The purple or blue gut color is shared by *Anoplodactylus latus*, a much larger pycnogonid which has not yet been found in Belize. The coloration of *A. imswe* indicates that it might feed on organisms containing blue-green algae, but since collecting data for this species do not contain information on habitat associates, its feeding preference remains unknown.

### *Anoplodactylus jonesi* Child, 1974

*Anoplodactylus jonesi* Child, 1974:497–500, fig 2; 1979:56, fig. 19a–b.

*Anoplodactylus (?) antillianus* Stock, 1975:1081–1082, fig. 57.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats in 0.5 m, coll. K. Rützler, 2 May 1974; 2♂.

**REMARKS.**—Both of these specimens are normal males with full ovigers and a tall tubular cement gland on each femur. Several questionable females have been found in the past that bear male ovigers, ova in the legs, and that lack cement glands. This seemingly abnormal situation has led to speculation on the status of this species in a genus in which the females are entirely without ovigers. Further discussion and figures of this species appear in Child (1979:56, fig. 19a–b).

**ECOLOGY.**—Habits and habitats are lacking for the Belizean specimen, but in Panama the species has been found most often among algae.

### *Anoplodactylus maritimus* Hodgson, 1914

*Anoplodactylus maritimus* Hodgson, 1914:164; 1915:148; 1927: 357.—Marcus, 1940:60.—Stock, 1975:1069–1074, fig. 54.

Not *Anoplodactylus maritimus*.—Hedgpeth, 1948:230, fig. 29d–e [= *A. iuleus* Stock, 1975:1069].

*Anoplodactylus parvus* Giltay, 1934:1–3, figs. 1–5.—Hedgpeth, 1948:223–224, fig. 27e–f.—Stock, 1951:13, figs. 14–16; 1954:127; 1955:235; 1957:85; 1975:1069–1074, fig. 54.—Bourdillon, 1955:590–591, fig. 1, pl. 1: fig. 2.—Fage and Stock, 1966:326.—Kraeuter, 1973:494–495.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats, coll. M. L. Jones, 6 Apr 1976; 1♀.

South Water Cay: Rubble from edge of chan-

nel in 6 m, coll. C. A. Child, 1 Feb 1978; 2♂ with eggs, 2 juveniles.

Twin Cays: NW coast, *Halimeda* mat from under mangroves in 0.3 m, coll. B. Kensley, 2 Feb 1978; 1♀.

**REMARKS.**—In agreement with Stock (1975: 1072), I have combined the two species under Hodgson's (1914) earlier designation. There is ample cause for confusion here as Hodgson's type was never figured. Giltay's (1934) *Anoplodactylus parvus* has been figured by several authors, including Giltay, but was never compared with Hodgson's type (which appears to have been lost). As presently designated, the species can also be easily confused with *A. petiolatus* (Kroyer), which itself is sufficiently variable to suggest the possibility of two species (Stock, 1975:1075). Stock (1975, figs. 53, 54) attempted to sort out and figure the differences between the present species and *A. petiolatus*.

Association with floating substrates has given this species an extremely wide distribution in the Atlantic. It has been found from Chesapeake Bay in Virginia, south to Bermuda and through the West Indies to Brazil. Hodgson (1914) originally described it from south of the Azores and it is known also from the Cape Verde Islands.

**ECOLOGY.**—This species is common over vast areas of the mid-Atlantic as one of the many inhabitants of the seaweed *Sargassum* (Bourdillon, 1955, fig 1). The type of *Anoplodactylus maritimus* was collected in *Sargassum*, and many other records confirm this association. I have also seen specimens feeding on hydroids attached to *Sargassum* dipped from Florida waters. The present collection, however, shows that this species occupies other habitats as well.

#### *Anoplodactylus monotrema* Stock, 1979

*Anoplodactylus robustus*.—Child and Hedgpeth, 1971:612–613 [literature].—Stock, 1975:1080.

*Anoplodactylus monotrema* Stock, 1979:15–18, figs. 4–5.—Child, 1979:56, 58, fig. 19c.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats in 0–1 m, coll. 7 Apr 1973; 1♂ with eggs.

**REMARKS.**—This species has a “fat” appear-

ance with a short blunt proboscis, abdomen, and ocular tubercle.

All specimens previously assigned to *Anoplodactylus robustus*, whether from European collections or from western hemisphere collections, were thought to agree. It recently became evident that the European specimens have more than one (usually 3) cement gland per femur whereas the American specimens have only one gland per femur. Other slight differences, when taken in combination, caused American specimens to be recognized as a separate species, *A. monotrema*. Therefore, the known distribution of the American species is confined to the east and west coasts of southern North America and northern South America, including the Galapagos Islands.

**ECOLOGY.**—The color of this littoral and sub-littoral species is usually straw or lighter. Its feeding habits are not yet identified. It has been taken on a wide variety of substrates.

#### *Anoplodactylus multiclavus* Child, 1977

*Anoplodactylus multiclavus* Child, 1977:593–596, fig. 4; 1979: 58, fig. 19d.

**MATERIAL EXAMINED.**—South Water Cay: SE side, in shallow grass bed with sand patches near *Rhizophora* stumps in 0.5 m, coll. J. Clark, 15 Jan 1976; 1♂ with eggs.

**REMARKS.**—This specimen agrees with the type, also a male, in all respects including the multiple cement glands, except that it appears slightly more robust.

**ECOLOGY.**—Both the type and this specimen have been found in association with or near mangroves.

#### *Anoplodactylus pectinus* Hedgpeth, 1948

*Anoplodactylus pectinus* Hedgpeth, 1948:234–236, fig. 34; 1954: 427.—Stock, 1955:235; 1974:17.—Arnaud, 1973:955–957.—Child, 1974:500; 1979:58.

*Anoplodactylus pectinis* [sic].—Stock, 1975:1050–1052, fig 41a.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats at tide line, coll. K. Rützler, 23 Apr 1974; 1♂. From *Dictyota* on reef flat in 0.5 m, coll. R. Larson, 16 Mar 1977; 1♂ with eggs, 1♂. Rubble

from sand trough behind outer reef ridge in 27 m, coll. C. A. Child, 6 Feb 1978; 3♂, 2♀. Rubble from just S of 6 Feb collection, in 27 m, coll. C. A. Child, 7 Feb 1978; 3♂.

Twin Cays: NW coast, mat of *Caulerpa verticillata* and mangrove rootlets beneath *Rhizophora*, intertidal, coll. C. A. Child, 2 Feb 1978; 1♀. Mat of *Halimeda* from nearby, intertidal, coll. B. Kensley, 2 Feb 1978; 1♀.

**REMARKS.**—This species, including its females, is easily recognized by the pectinate major heel spine that can be seen under high magnification.

This marks the second time *Anoplodactylus pectinus* has been collected in the western Caribbean. Previously, it has been collected on the Caribbean coast of Panama, in Florida, the Caribbean Leeward Islands, and in Madagascar.

**ECOLOGY.**—Freshly killed specimens had light green intestinal diverticula. This color may be a character useable to distinguish fresh specimens of this species, at least on the Belizean barrier reef. *Anoplodactylus portus* shares this green color, but retains coloration even after long storage, unlike *A. pectinus*. The color is undoubtedly a function of diet, although the particular green food matter is unknown.

### *Anoplodactylus portus* Calman, 1927

*Anoplodactylus portus*.—Stock, 1975:1052–1053, fig. 41b–e [literature].—Child, 1978:133–144, figs. 1–4; 1979:58–59.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Rubble and *Halimeda* from reef crest in 0.5 m, coll. C. A. Child, 29 Jan 1978; 1♂ with eggs. Lagoon flats, with *Syringodium* and sediment in 1.2 m, coll. B. Kensley, 1 Feb 1978; 1♂ juvenile, 1 larva. Mixed algae and compact corallines at shore, coll. B. Kensley, 5 Feb 1978; 1♀ juvenile. *Halimeda* and rubble from outer reef ridge in 18 m, coll. B. Kensley, 7 Feb 1978; 1♀ juvenile.

South Water Cay: Rubble from edge of channel in 6 m, coll. C. A. Child, 1 Feb 1978; 1♂, 2♀.

Twin Cays: NW coast, mat of *Caulerpa verticillata* and mangrove rootlets under *Rhizophora*, intertidal, coll. C. A. Child, 2 Feb 1978; 1♀.

**REMARKS.**—This is a pantropical species with

a robust appearance which aids in distinguishing it from the many other tropical species of this genus. As with all species of *Anoplodactylus*, the configuration of the male femoral cement gland(s) is a key character. In conjunction with oviger, chela, and propodus characters, it facilitates recognition among these otherwise difficult species. This observation does not hold for females, which remain difficult if not impossible to identify if they are not taken in the same sample or area with recognizable males.

**ECOLOGY.**—This species is often collected with gut diverticula in the legs showing green chloroplasta or at least chlorophyllous coloration ingested from the algal habitat in which it is often found. Whether or not it picks this up directly as food or as a biproduct of eating algal-grazing fauna has never been demonstrated.

### *Anoplodactylus* sp.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats, coll. K. Rützler, 4 May 1974; 1♀ juvenile. Lagoon surface among *Thalassia* and *Sargassum*, coll. R. Larson with plankton net, 25 Jan 1978; 1 larva. Tidal flat, plankton net resting on bottom in 0.5 m, coll. R. Larson, 30 Jan 1978; 1 larva. With *Syringodium* in 1.0–1.5 m, coll. B. Kensley, 3 Feb 1978; 2♀ juveniles.

**REMARKS.**—None of these specimens is mature enough to identify.

## Family ENDEIDAE

### *Endeis* Philippi, 1843

#### *Endeis spinosa* (Montagu, 1808)

*Endeis spinosa*.—Hedgpeth, 1948:238–240 [early literature].—Stock, 1952b:185–186; 1954:128; 1957:85; 1962:218; 1968a:59 [key]; 1968b:32, fig. 25.—Soyer, 1966:3.—de Haro, 1966:9; 1967:109, 112–113, fig. 5.—Krapp, 1973:72.—Child, 1979:66.

**MATERIAL EXAMINED.**—Carrie Bow Cay: *Thalassia* beds in lagoon, 1.5 m, coll. J. D. Ferraris, 11 May 1975; 1♂ with eggs.

Stann Creek: Surface plankton tow off Pelican

Beach, 0.5 mi out, coll. R. Larson, 13 Apr 1978; 1♀.

**REMARKS.**—This species has been found from Norway to Argentina, including the Mediterranean Sea, at mainly littoral and sublittoral depths.

**ECOLOGY.**—*Endeis spinosa* is a frequent inhabitant of floating *Sargassum* in the Caribbean and elsewhere. It is also common in *Thalassia* grass that is supporting colonies of hydroids, bryozoans, and ascidians.

### Family NYMPHONIDAE

#### *Nymphon* Fabricius, 1794

##### *Nymphon floridanum* Hedgpeth, 1948

*Nymphon floridanum* Hedgpeth, 1948:196–199, fig. 17 [long-necked form only].—Stock, 1955:215, fig. 1a [long-necked form only]; 1975:994–998, figs. 14–15.—Kraeuter, 1973: 494.—Krapp and Kraeuter, 1976:336–337.—Child, 1979: 37.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Tidal flats at low water, coll. K. Rützler, 23 Apr 1974; 1♂. Tidal flats, coll. M. L. Jones, 5 Apr 1976; 1♀. *Halimeda* and rubble from outer reef ridge in 18 m, coll. B. Kensley, 7 Feb 1978; 1 juvenile.

**REMARKS.**—These specimens are all the long-necked form of *N. floridanum* (*sensu strictu*) as defined by Stock (1975:994–998). In this extensive genus, this species (along with its look-alike, *N. aemulum*) is one of the few tropical members that is both littoral and sublittoral. It is known from Georgia through the Caribbean to as far south as French Guiana. It has been found in association with coral, algae, and sandy habitats.

### Family RHYNCHOTHORACIDAE

#### *Rhyncothorax* Costa, 1861

##### *Rhyncothorax architectus* Child, 1979

*Rhyncothorax architectus* Child, 1979:68–72, figs. 23, 24a–g, 25a–e.

**MATERIAL EXAMINED.**—Carrie Bow Cay: Broken rock and rubble at tide line on ocean side, coll. J. Clark, 17 Jan 1976; 1♂.

**REMARKS.**—This is the third capture locality for this variable species, the first two being the Caribbean and Pacific sides of the Isthmus of Panama. This specimen agrees well with male paratype specimens from Panama. It has low middorsal tubercles instead of the taller ones of the holotype. The species is known only from the intertidal.

**ECOLOGY.**—This species probably came from the coral sand around or under rock rubble. The most common habitats of this genus, as reported in the literature, are interstitial, with the animals living between sand grains around or under rocks. The above capture probably substantiates this mode of living and suggests that coralline and coral sand are the primary substrates.

### *Rhyncothorax crenatus*, new species

FIGURE 167

**MATERIAL EXAMINED.**—Carrie Bow Cay: Coral sand and rubble in sand trough behind outer reef ridge in 27 m, coll. C. A. Child, 6 Feb 1978; 1 subadult specimen, holotype (USNM 170996).

**DESCRIPTION.**—Trunk compact, first 2 segment lines complete, third lacking. First 3 trunk segments with tall conical median dorsal tubercles almost as tall as ocular tubercle. Surface of entire animal except proboscis with minute scattered papillae. Dorsal and ventral trunk surfaces with pattern of lightly pigmented molt sutures similar to reticulations. Ocular tubercle tall, pointing about 30 degrees anteriorly, with 2 tiny lateral tubercles flanking a conical cap, a posterior triangular median tubercle and 2 thin short tubercles lateral and posterior to triangular tubercle. Conical cap with single posterior seta. Eyes large with medium dark pigment. Abdomen extending to tip of second coxae of fourth legs, cylindrical, and with proximal and distal constrictions, armed with 3 dorsodistal setae.

Proboscis cylindrical-conical, with 2 dorsolateral bulges flanking a tall spike-like tubercle in median line halfway along proboscis. Mouth with 2 laterally flattened antimeres confining it to a vertical slit.

Palps 4-segmented, arising from rather long

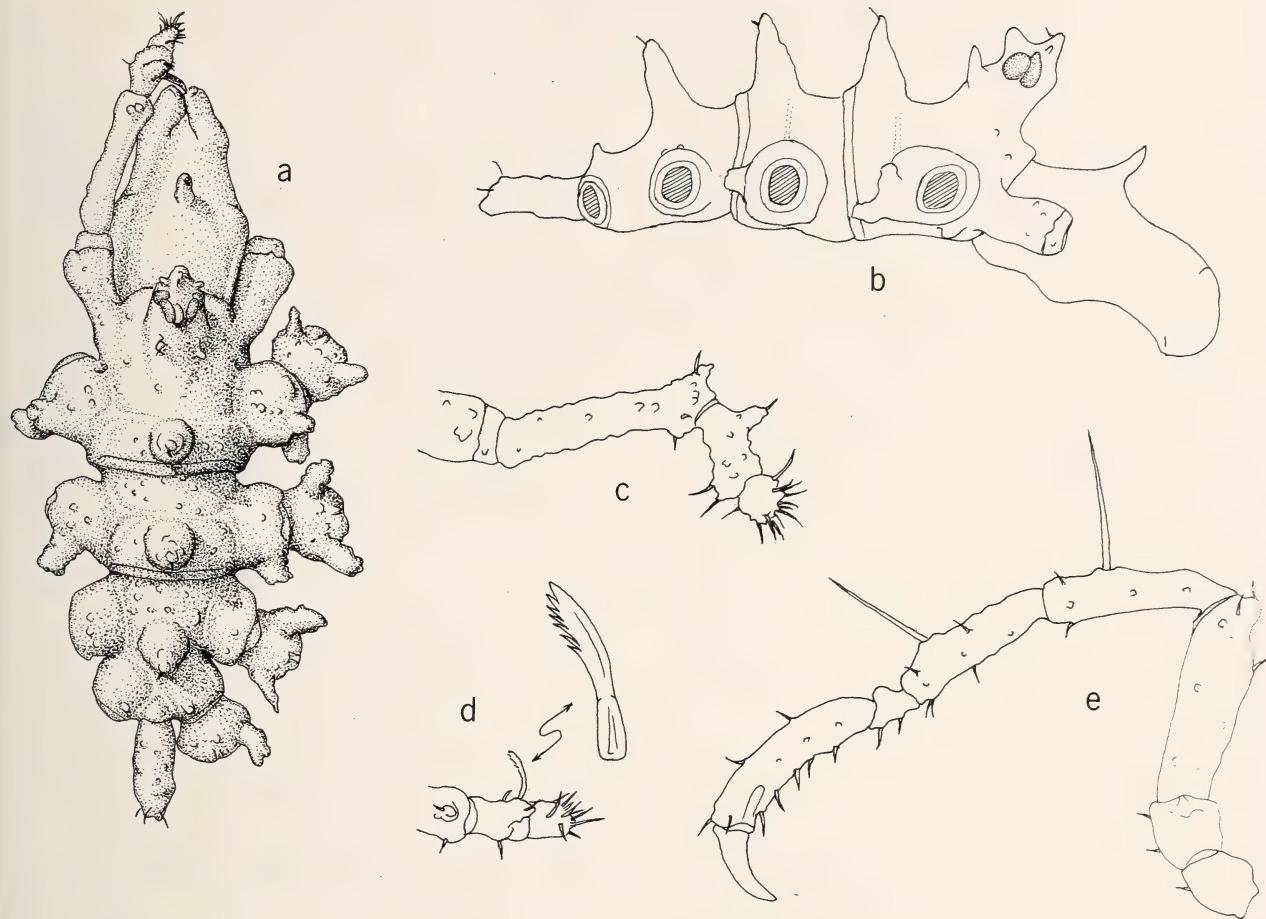


FIGURE 167—*Rhynchothorax crenatus*, new species (holotype): *a*, trunk; *b*, trunk, lateral; *c*, palp; *d*, terminal segments of palp, dorsally, with enlargement of endal spine; *e*, third leg.

trunk tubercle bases lateral to and closely set against proboscis. First segment very short, half as long as its diameter. Second segment longest, with small triangular dorsodistal tubercle armed with 2–3 setae and tiny ventrodistal tubercle armed with single seta. Third segment slightly less than half as long as second, with narrow median dorsal tubercle armed with seta, and small ventrodistal bulge armed with 2–3 setae. Terminal segment round in lateral aspect, armed with many setae dorsally, distally, and ventrally. Third palp segment armed on endal surface with single large spine bearing denticulations on posterior surface only. Spine slightly longer than diameter of segment.

Chelifores entirely lacking.

Oviger incomplete (?) or vestigial (?) in hol-

type, only small unsegmented bud present.

Legs moderately thin, armed with a few short setae and a very long single seta on first and second tibiae. Femora lacking long setae. Femur the longest segment; first and second tibiae each shorter than preceding segment. Major leg segments of anterior 4 legs slightly longer than posterior four. Tarsus with single ventral spine and seta. Propodus without heel, moderately curved, armed with 5–6 sole spines. Terminal segments of anterior 4 legs armed with 4–6 tarsus setae and up to 12 sole spines. Claw robust, less than half propodus length. Auxiliary claws lacking.

**DISTRIBUTION.**—Known only from the type-locality, Carrie Bow Cay, Belize, in a depth of 27 meters.

**ETYMOLOGY.**—From Latin, meaning notched,

in reference to the appearance created by the median trunk, ocular, and proboscis tubercles in lateral view.

**MEASUREMENTS (mm).**—Trunk length (tip of ocular tubercle to tip of fourth lateral processes), 0.65; trunk width (across first lateral processes), 0.42; abdomen length, 0.14; proboscis length, 0.35; third leg, coxa 1, 0.1, coxa 2, 0.08, coxa 3, 0.07, femur, 0.23, tibia 1, 0.2, tibia 2, 0.17, tarsus, 0.05, propodus, 0.21, claw, 0.09.

**REMARKS.**—This subadult specimen (sex pores not evident) has a unique set of characters although it superficially resembles *Rhyncothorax unicornis* Fage and Stock from the Cape Verde Islands. The trunk of *R. crenatus* is thinner, with more widely spaced lateral processes. None of the appendage tubercles are nearly as long or thin, the ocular tubercle is very different with its cone and posterior tubercles, and the median trunk tubercles are simple cones instead of complex tuberculate and papillose tubercles.

On the other hand, there are several striking similarities between the two species. Both share a single mid-dorsal proboscis tubercle, both have similar propodus configuration except for the strong distal sole spine of *Rhyncothorax unicornis*, and both have similar palps although the tall tubercle of the second segment and the tiny terminal segment are not present on *R. crenatus*. Both species lack auxiliary claws and have lateral process and coxa 1 tubercles in the same places although their sizes are very different. Finally, both species have small lateral tubercles placed behind the ocular tubercle and rudimentary ovigers (signifying that both are females?) of a button-like appearance.

The two species are similar enough perhaps to form a geminate pair, separated by the Atlantic Ocean and Caribbean Sea. Probably, each is a valid species, but the discovery of a specimen intermediate between the two, if such exists, would invalidate any suggestion that these examples represent speciation by geographic isolation due to plate tectonics. Although the male ovigers in *Rhyncothorax* species are much alike, it might be worthwhile to study the character of

male ovigers in these two species when more specimens are collected.

Thompson (1909:535) first proposed a separate family for this genus and I concur that its combination of characters fit none of the currently accepted genera with which it has been placed.

## Conclusions

The pycnogonid fauna of Carrie Bow Cay and its vicinity on the Belizean barrier reef is extremely rich. Extensive collecting during this study has produced approximately 300 specimens from mainly littoral habitats. Thirty-one identified species in 14 genera are represented, including four new species. The habitat diversity on the reefs makes it probable that collecting in nearby unsampled areas will further increase this number. For instance, two samples taken from a single mangrove habitat on different days contained no less than 10 species of pycnogonids, and five small samples of rubble and algae from depths of 18 and 27 meters on the outer reef yielded nine species.

Algae appear to be a preferred habitat but seldom is an alga associated with just one species of pycnogonid. *Sargassum* is regularly colonized by *Anoplodactylus maritimus*, *Endeis spinosa*, *Tanystylum tubirostrum*, *Numphopsis duodorsospinosum*, and occasionally other species. All these species, however, are also found in other habitats, such as rubble, other algae, sea grass, coral, and mangrove roots. Without an analysis of gut content there is no proof that pycnogonids ingest algae. More likely, they eat the soft parts of animals living on the algae or on rubble having associated algal growth. Specimens of *Achelia sawayai*, for example, were captured on rubble with algae supporting sessile organisms and were not found on "clean" algae collected at the same time. Pycnogonids with green intestinal diverticula (*Anoplodactylus pectinus* and *A. portus*) possibly form the second step in the food chain by ingesting the tissues of animals that feed primarily on green algae. Pycnogonids move very slowly so that it is almost impossible for them to feed on mobile fauna. A stand of foliose

TABLE 27.—Geographical distribution of Belizean pycnogonid species

Species	Pantropical	Middle America (Pacific)	Galapagos Islands	Panama (Caribbean)	Belize	Other Caribbean	Western N Atlantic	Guianas and Brazil	W Africa and Europe	Indian Ocean
<i>Achelia sawayai</i>			X	X X X		X	X	X	X	X
<i>Ammothella appendiculata</i>	X		X	X X X		X	X	X	X	X
<i>A. exornata</i>		X	X	X X X		X				
<i>A. marcusii</i>	X	X	X	X X X		X				
<i>A. rugulosa</i>			X	X X X		X		X		
<i>Ascorhynchus latipes</i>			X	X X X		X			X	
<i>A. serratus</i>				X? X						
<i>Eurycyde raphiaster</i>			X	X X X		X	X	X	X	
<i>Hedgpethius mamillatus</i>				X						
<i>H. tridentatus</i>				X		X				
<i>Nymphopsis duodorsospinosa</i>	X		X	X X X		X				
<i>Tanystylum birkelandi</i>			X	X						
<i>T. tubirostrum</i>	X			X X		X				
<i>Callipallene belizae</i>				X						
<i>C. emaciata</i>				X X X		X	X	X	X	
<i>Parapallene bermudensis</i>				X		X				
<i>Pigromromitus timsanus</i>	X									
<i>Anoplodactylus bahamensis</i>				X		X				
<i>A. batangensis</i>	X									
<i>A. evelinae</i>		X		X X X		X	X	X	X	
<i>A. imswee</i>				X						
<i>A. jonesi</i>				X X X		X				
<i>A. maritimus</i>				X X X		X		X	X	
<i>A. monotrema</i>		X		X X X		X		X		
<i>A. multiclavus</i>				X X X						
<i>A. pectinus</i>				X X X		X				X
<i>A. portus</i>	X									
<i>Endeis spinosa</i>				X X X		X	X	X	X	
<i>Nymphon floridanum</i>				X X X		X		X		
<i>Rhynchothorax architectus</i>	X			X X						
<i>R. crenatus</i>				X						

green algae can support an enormous number of attached organisms, many of which are known to be food for pycnogonids. Among these organisms are hydroids—long a classic example of pycnogonid food—sponges, tube worms, ascidians, and anemones. Since Pycnogonids have been captured on living corals, they probably also feed on these cnidarians.

Most of the Belizean species have a littoral depth distribution with the exception of *Parapallene bermudensis* which has only been captured within the narrow limits of 27 to 33 meters. This rarely collected species may have escaped owing to inefficient collecting techniques. More sampling on reefs at this depth range may provide many other species previously thought to be rare.

The geographical distribution of pycnogonids from Belize is summarized in Table 27. Most of the species also occur in the eastern Caribbean and some are present along the Caribbean shores of Panama. Three species were found in the Caribbean for the first time: *Hedgpethius tridentatus*, previously known from Florida; *Anoplodactylus bahamensis*, Bahamas; and *Parapallene bermudensis*, Bermuda. The four new species presented here are known only from Belize. Nineteen species are known from the western North Atlantic beyond the Caribbean, and at least 10 range to the

Guianas and Brazil. There are eight known amphi-Atlantic species, two of which are also known from the Indian Ocean. The Pacific distribution of Belize species is much more restricted, as is to be expected. The isthmian barrier has permitted colonization of only six species on the Pacific shores of Central America. Two species are also known from the Galapagos Islands and one of these has been captured in other areas of the Eastern Pacific. Three additional species are pantropical in distribution and are known from most of the above localities.

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# *Pontomyia* Edwards (Diptera: Chironomidae), a Member of the Coral Reef Community at Carrie Bow Cay, Belize

Gernot Bretschko

## ABSTRACT

The occurrence of the genus *Pontomyia* (Chironomidae, Tanytarsini) in the Caribbean Sea is reported for the first time. Larvae were found around Carrie Bow Cay, Belize, in the lagoon, on the reef flat, on the fore reef and along the fore-reef slope to a depth of 25–30 m (maximum sampling depth). Distribution of larvae indicates that *Pontomyia* is a true member of the off-shore benthic community. Pupal skins and females closely resembling those of *P. natans* Edwards, 1926, were common in plankton samples. Species identification is not possible, however, because no males were found.

## Introduction

Previous studies have reported species of the genus *Pontomyia* from only Pacific locations. It was first found in Samoa by Buxton (1926), whose collection was described by Edwards (1926). Characteristic features of the genus are larvae that morphologically resemble normal Tanytarsini larvae, a highly specialized adult male, and a completely reduced female that lacks all appendices on head and thorax except inoperative stumps of the second and third pairs of legs. Buxton (1926) reported that the species he studied, *P. natans*, spends its entire life-cycle under water, that males swim with their legs, and that females do not leave their pupal housings.

Another species, *Pontomyia pacifica*, was described from Japan by Tokunaga (1932), whose detailed field observations and laboratory experiments revealed that males of *P. pacifica* are unable to swim. They are true surface gliders propelled by their wing activity. Like the males, females emerge on the water surface, where they await copulation with a male passing by.

Recently, Hashimoto (1959) showed that the biology of *Pontomyia natans* is very similar to that of *P. pacifica* in that adults are confined to the surface and are unable to copulate while submerged. Flying males of *P. natans* have been reported from the Red Sea and from northeast Australia (Thienemann, 1974).

Larvae of *Pontomyia* have been found in association with various algae and in sandy mud below plant beds (Tokunaga, 1932; Hashimoto, 1959). All marine chironomid species are reported to be restricted to the intertidal zone; only *P. natans* has been found below the extreme low water level (Hashimoto, 1976), but always near the shore (Hashimoto, 1962). This author concluded that “in site of the excellent adaptation to the open sea, the territories of *Clunio* and *Pontomyia* are confined to the coast” (1962:241).

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## Study Area and Methods

Sampling for this study took place in May 1977 around Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ) a small island on the Caribbean barrier reef off Belize (Rützler and Macintyre, herein: 9) Benthic samples (Figure 168) were taken in the *Thalassia* stands between patch reefs in the lagoon, and from sand substrates on the fore reef, including sand trough and fore-reef slope, to a depth of about 25–30 meters. All samples were qualitative; two to three liters of sediments were brought to the laboratory in a plastic bag and subsequently were well mixed with sea water in a bucket. After a few hours, the bottom layers in the bucket became anoxic, and chironomid larvae swam to the surface and were collected. Chironomid larvae were also present in four semiquantitative samples taken on the reef flat by K. Rützler in April–May 1974.

Seventy-one quantitative plankton tows (250  $\mu m$  mesh size, water depth of 0.–0.5 and 2.5–3.0 m) were taken by J. D. Ferraris (herein: 143) parallel to the reef, in the lagoon and outside the

fore-reef slope, and during different lunar and tidal phases, in April–May 1976 (Figure 168). Nets were towed horizontal distances that varied from 200 to 552 m, and the volume of water filtered per tow ranged from 13.2 to 36.4  $m^3$ .

## Results and Discussion

Out of 13 large benthic samples, 11 contained chironomid larvae and a few females (Figure 169). Chironomids were absent only in one sample of coarse sand from inside of a patch reef and in one sample of detached *Thalassia* seagrass leaves. The positive samples included muddy sands—with and without *Thalassia*—from the lagoon (2–5 m deep), coral rubble from the reef flat (0.5 m), and fine sands from the fore reef (3–23 m) and along the reef drop-off (12–30 m) Figure 168). Although the abundance of larvae is rather low everywhere, it is slightly higher in the lagoon. In the semiquantitative reef-flat samples densities range from about 10 to 150 larvae/ $m^2$  and are comparable to plankton samples having maximum counts of 2.2 pupal skins/ $m^3$  in the lagoon

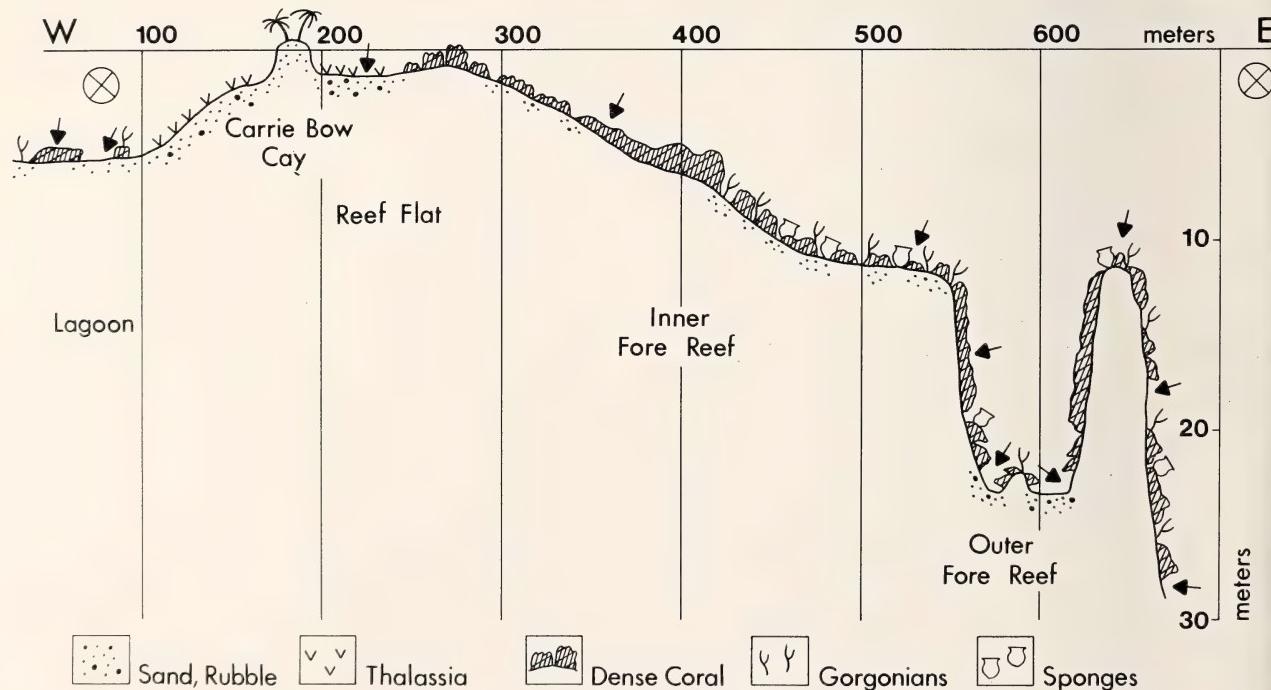


FIGURE 168.—Transect across Belizean barrier reef near Carrie Bow Cay indicating sample locations (circle = plankton tow, arrow = benthic sample).

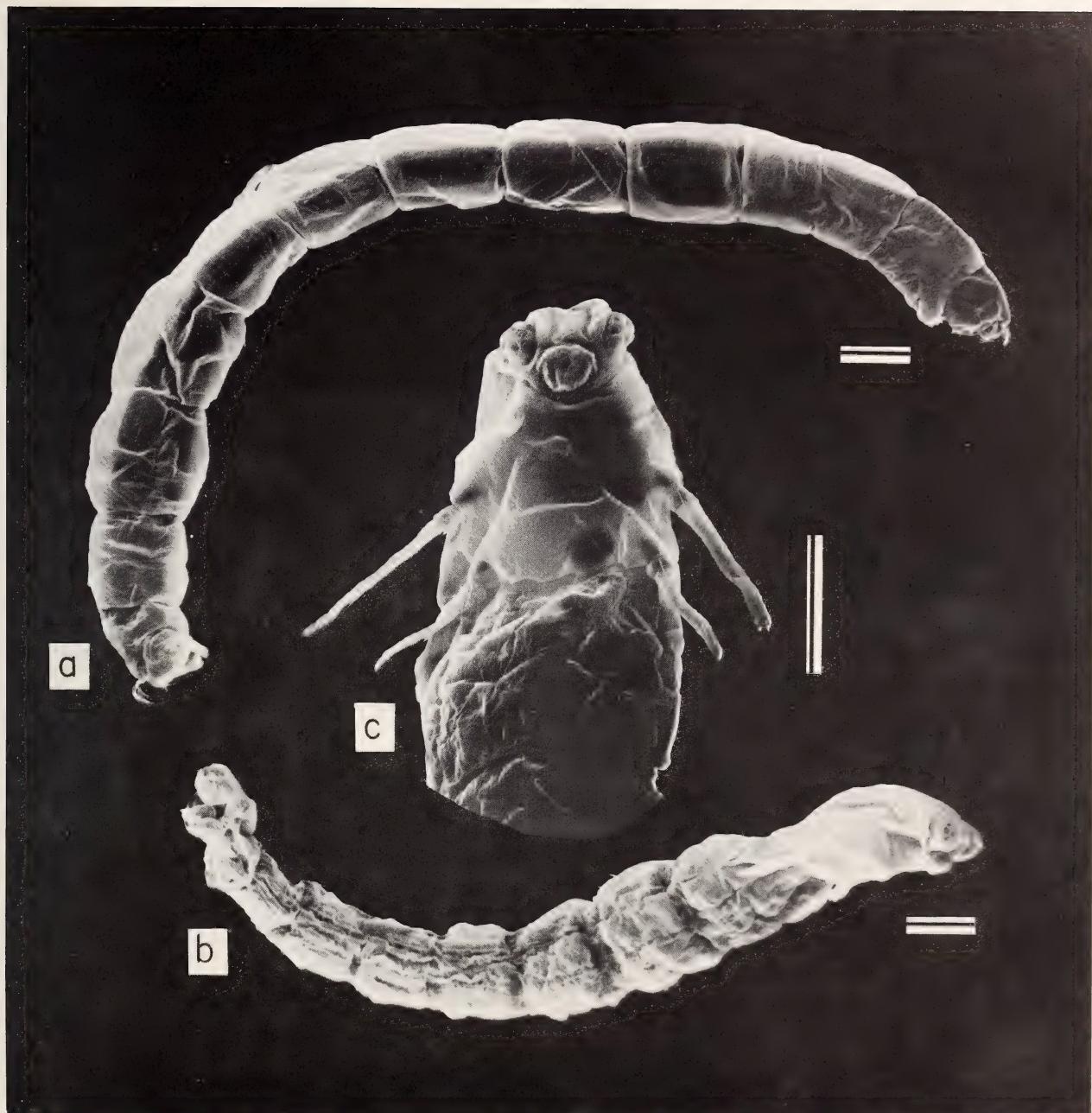


FIGURE 169.—*Pontomyia* sp., scanning electron micrographs: *a*, larva, fourth instar; *b*, female, vermiciform body somewhat shrunk; *c*, front end of female, with eyes and first two pairs of legs largely reduced, mouthparts, wings, and last pair of legs absent (scales = 200  $\mu\text{m}$ ).

and 0.4/m<sup>3</sup> along the drop-off. The wide distribution of *Pontomyia* sp. around Carrie Bow Cay and its occurrence in relatively deep waters clearly indicates—contrary to earlier reports—

that this chironomid species is a member of the marine offshore benthic community.

The occurrence in the samples of all developmental stages at the same time suggests continu-

ous reproduction. Analysis of 273 specimens indicated the absence of males, which in such a large sample points to a parthenogenetic population—a characteristic previously unknown for members of the genus *Pontomyia*.

Thirty-four plankton samples contained skins of chironomid pupae and a few partly macerated females. Considerably more pupal skins were present in planktonic samples from the lagoon than in samples from the outer fore-reef ( $t = 3.882$ ,  $d.f. = 34$  for 0.0–0.5 m depth; and  $t = 4.772$ ,  $d.f. = 33$  for 2.5–3.0 m depth, respectively). These results support the findings drawn from the qualitative benthic samples. A correlation with moon phases and tide could not be established. A distinct relationship, however, exists between the abundance of exuviae and the diurnal cycle: pupal-skin density is significantly higher in samples taken between 1800 and 2400 h compared to samples taken at all other 6-hour intervals ( $t = 3.803$ – $4.786$ ,  $d.f. = 29$ – $37$ , for all samples taken together). Surface tows (0–0.5 m) yielded more chironomids at all times of day than did tows from depths of 2.5 to 3.0 m (lagoon:  $t = 1.883$ ,  $d.f. = 37$ ; off fore-reef slope:  $t = 4.999$ ,  $d.f. = 30$ ). The specific gravity of the pupal skins may well be the reason for these differences.

Of the four species described for the genus *Pontomyia*, *P. cottoni* Womersley (1937) was thought to be a junior synonym of *P. natans* Edwards (Hashimoto, 1959). In a recently pub-

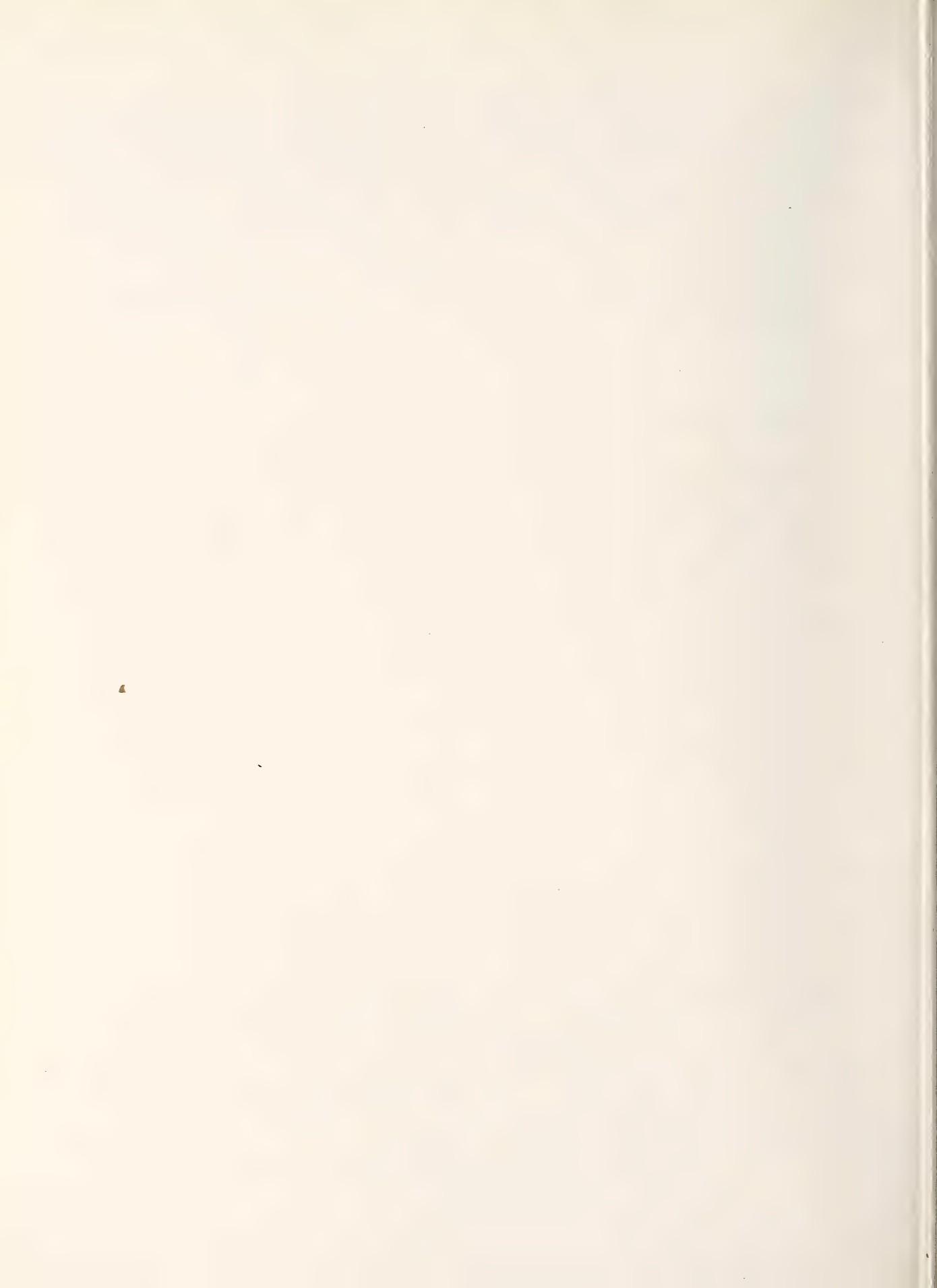
lished paper (Cheng and Hashimoto, 1978), the species *P. cottoni* is listed, yet without further taxonomic comments. Morphological differences between *P. cottoni* and *P. natans* are still considered of doubtful value (Hashimoto, 1973) but from an ecological point of view *P. cottoni* could be separated as a dweller of rather shallow water and tide pools (H. Hashimoto, pers. comm., 1979). The remaining three species are *P. natans* Edwards (1926), *P. pacifica* Tokunaga (1932), and *P. oceana* Tokunaga (1964). Immature stages and females, in addition to the males, are described for *P. pacifica* and *P. natans*. The larvae described for *P. natans* may not belong to *Pontomyia* at all, but to some other species of the Tanytarsini group (Tokunaga, 1932).

This is the first observation of a *Pontomyia* species outside the Indo-Pacific region. Confident specific identification of the present material (larvae, pupal skins, a few females) is not possible because chironomid taxonomy is based on the morphology of the adult male which has not yet been found in the Caribbean population. The presence of four joints on the female leg excludes *Pontomyia oceana* and *P. pacifica*, although the larval antennae resembles the latter species more than the remaining *P. natans*. If we are dealing with a new species it is probably most closely related to *P. natans*. The taxonomic status of *P. cottoni* might require further collection and reevaluation.

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# Ophiuroidea (Echinodermata) from Carrie Bow Cay, Belize

Frederick H. C. Hotchkiss

## ABSTRACT

Thirty-six species of ophiuroids representing 16 genera in eleven families occur at Carrie Bow Cay, Belize. The rank order of abundance of species in various parts of the reef complex is estimated on the basis of numerical representation in the collection. The four most common species in the lagoon among discarded conch shells are *Ophiothrix oerstedi*, *Ophiactis savignyi*, *Ophiothrix angulata*, and *Ophiolepis paucispina*; on the reef flat are *Ophioderma appressum*, *Ophiocoma echinata*, *Ophiolepis impressa*, and *Ophiocoma wendti*; on the reef crest are *Ophiocoma wendti*, *Ophiocoma paucigranulata*, *Ophiocoma pumila* and *Ophiocoma echinata*; on the fore reef including the accessible part of the fore-reef slope are *Ophiocoma pumila*, *Ophiothrix angulata*, *Ophioderma rubicundum*, and *Ophiurochaeta littoralis*. Fifteen species are reported for the first time from Belize, including a new species of *Ophioderma*. All specimens of *Ophiostigma* sp. are six armed and fissiparous; they almost certainly represent a new species different from *O. isacanthum*. The occurrence of young in the bursae of *Ophiurochaeta littoralis* and *Ophiolepis paucispina* indicates but does not prove viviparity. A small amphiuroid that clings mouth to mouth to an *Ophiopsila riisei* has three arms aligned and in contact with those of its host. The blue-purple color of many preserved specimens of *Ophiothrix angulata* and *O. oerstedi* is an artifact, the color in life usually being shades of brown.

## Introduction

This report on the ophiuroids of Carrie Bow Cay is based on field work conducted 21 April

through 9 May 1974. Carrie Bow Cay is a small island situated 22 km southeast of Dangriga (Stann Creek) (approximately 16°48'N, 88°-05'W), on the barrier reef that extends along the coast of Belize (formerly British Honduras). An extensive collection of ophiuroids was made from various habitats and depths for the purpose of inventorying the species composition and distribution. The principal collecting localities categorized by major physiographic features of the reef complex are listed below. Detailed descriptions of these habitats are given by Rützler and Macintyre (herein: 9).

Thirty-six species in 16 genera and 11 families of ophiuroids are recognized in this report, including two not fully identified and one that is a new species of *Ophioderma*. All the species collected by Devaney (1974) at Turneffe Islands, Lighthouse Reef, and Glover's Reef are represented at Carrie Bow Cay except, perhaps, his *Ophioderma* sp., which I could not recognize from his description. Fifteen of the species are reported from Belize for the first time, although they have been known from other West Indian localities. Almost all species were photographed in color while alive, in order to document colors that are lost or changed with the fixatives used.

**ACKNOWLEDGMENTS.**—My participation in this project was made possible by a Smithsonian Postdoctoral Fellowship (1973-1974). The field party consisted of K. Rützler, E. Kirssteuer, K. Sandved, B. Spracklin, and myself. K. Sandved took the color photographs in the field and collected many ophiuroids. The completion of this manuscript was facilitated by the assistance of J. Jonigian, M. Roberson, T. Burrows, J. Arguelles, E. Ball, D. DeJianne, A. Pruzan, and by a Short-Term

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Visit Program award from the Office of Academic Studies, Smithsonian Institution.

## Methods

Ophiuroids were collected at 13 stations by hand using snorkel or SCUBA, according to depth. In most cases specimens were found hidden under coral, coral rock, or dead shells, or in nooks and crannies of living coral or sponges. Bulk samples of substrate for sorting ashore were collected from stations 1, 10, 12, and 13. Live specimens were photographed with 35 mm color slide film and electronic flash illumination in temporary aquaria or in trays. Specimens were relaxed in magnesium chloride solution judged isotonic with sea water by optical refractometer readings. Specimens were fixed in 10% formalin in sea water (4% formaldehyde solution) neutralized and buffered with 20 g/l hexamethylenetetramine and transferred to 70% ethanol on return to the National Museum of Natural History. Most of the material has been kept in alcohol for future dissection and histological analysis, but some specimens were dried for identification purposes. Photographs and voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the United States National Museum (USNM), uncataloged material designated CBC.

## Station List

(Station numbers keyed to Figure 170)

### Lagoon

1. Northwest side of cay, foot of pier; among discarded conch shells, 0.5 m.
2. Southwest end of cay; rubble area between sand and *Thalassia*, 0.5 m.

### Back Reef

3. Main reef transect; patch-reef zone, 1 m.

### Reef Flat

4. Northeast end of cay; *Penicillus* zone, 0.5 m.
5. Southeast end of cay; *Penicillus* zone, 0.5 m.
6. Coral-head/coral-pavement zone, 1 m.
7. Inner reef-crest zone, 0.5 m.

### Reef Crest

8. Coral-rubble berm (storm ridge), intertidal to 0.5 m (Plate 5: top left).
9. Outer reef-crest zone, 0.5 m.

### Inner Fore Reef

10. High-relief spur and groove zone, along the reef transect; bulk sample, 10–12 m.

### Outer Fore Reef

11. Sand trough near transect; bottom of shoreward slope of outer ridge, 24 m.
12. Outer ridge near transect; bulk sample, 12 m.
13. Fore-reef slope near transect; bulk sample, 26 m; incidental 1973 samples, 15–28 m.

## Species List

(\* = new records for Belize)

### Superfamily OPHIUROIDEA

#### Family GORGONOCEPHALIDAE

\**Astrophyton muricatum* (Lamarck)

#### Family OPHIOMYXIDAE

*Ophiomysxa flaccida* (Say)

#### Family OPHIACANTHIDAE

\**Ophiometrella glabra* (H. L. Clark)

#### Family HEMIEURYALIDAE

\**Sigabeia murrhina* Lyman

#### Family AMPHIURIDAE

\**Amphiura fibulata* Koehler

\**A. stimpsonii* Lütken

\**Axiognathus squamatus* (Delle Chiaje)

\**Ophiostigma* sp.

#### Family OPHIACTIDAE

\**Ophiactis algicola* H. L. Clark

#### Family OPHIOTRICHIDAE

*O. savignyi* (Müller and Troschel)

*Ophiothrix (Acanthophiothrix) suensonii* Lütken

*O. (Ophiothrix) angulata* (Say)

*O. (Ophiothrix) lineata* Lyman

*O. (Ophiothrix) oerstedi* Lütken

#### Family OPHIONEREIDAE

*Ophionereis reticulata* (Say)

\**O. squamulosa* Koehler

#### Family OPHIOCOMIDAE

*Ophiocoma echinata* (Lamark)

*O. paucigranulata* Devaney

*O. pumila* Lütken

*O. wendti* Müller and Troschel

\**Ophiocomella ophiactoides* (H. L. Clark)

\**Ophiopsila risci* Lütken

#### Family OPHIODERMATIDAE

\**Ophioderma anitae*, new species

*O. appressum* (Say)

*O. brevicaudum* Lütken

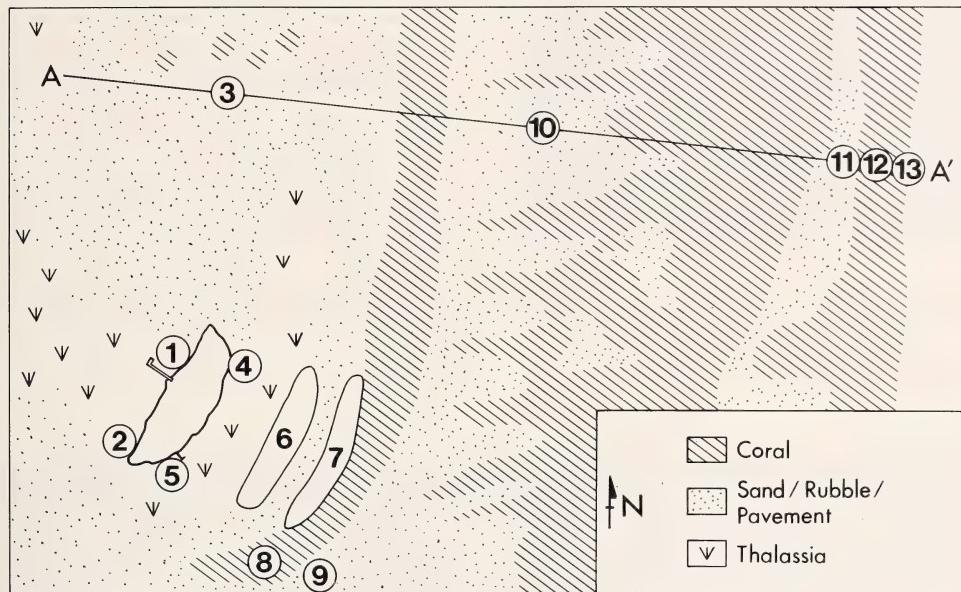


FIGURE 170.—Sketch map of collecting stations described in text (1, 2 = lagoon, 3 = back reef, 4–7 = reef flat, 8, 9 = reef crest; 10 = inner fore reef, 11–13 = outer fore reef; A–A' = study transect).

\**O. brevispinum* (Say)

*O. cinereum* Müller and Troschel

\**O. guttatum* Lütken

*O. phoenium* H. L. Clark

*O. rubicundum* Lütken

\**O. squamosissimum* Lütken

*Ophioderma* sp.

*Ophioderma* sp. juv.

*Ophiurochaeta littoralis* (Koehler)

#### Family OPHIURIDAE

*Ophiolepis impressa* Lütken

*O. paucispina* (Say)

### Superfamily OPHIUROIDEA

#### Family GORGONOCEPHALIDAE

##### ***Astrophyton muricatum* (Lamarck)**

*Euryale muricatum* Lamarck, 1816:538.

*Astrophyton muricatum*.—Agassiz, 1835:172.—Müller and Troschel, 1842:122.—Lütken, 1859:258; 1869:68, 106.—Lyman, 1865:192.—Ljungman, 1866:336.—Verrill, 1867: 341; 1899a:84; 1899b: 381.—Döderlein, 1911:7, 18, 53, 108, pl. 5: fig 1; 1927:24, 25.—H. L. Clark, 1915:188; 1919:56, 71; 1933:34, 42.—A. H. Clark, 1922:210.—Boone, 1933:103.—Engel, 1939:4.—Fontaine, 1953: 200.—John and Clark, 1954:140.—Cherbonnier, 1959:

261.—Fell, 1960:8.—Parslow and Clark, 1963:43.—Davis, 1966:435.—Roa, 1967:283.—Fricke, 1968:1.—Tommasi, 1970:11, pl. 2: fig. 3.—Godcharles and Jaap, 1973:56.—Zeiller, 1974:106 [color fig.].

*Astrophyton costosum*.—Lyman, 1865:192; 1882:256, 257, 266, 271, 290, 313, 326, pl. 35: figs. 17–25.—Nutting, 1895: 172.—Koehler, 1907:349.

*Astrophytum muricatum*.—A. H. Clark, 1921:52; 1954:376.

**MATERIAL DEPOSITED.**—USNM E17735 (1 spec.); USNM E19478 (1 spec.).

**DISTRIBUTION.**—One specimen was secured from a coral sample taken in 10–12 m in the spur and groove zone of the inner fore reef along the main study transect (station 10); the other specimen was collected by B. Spracklin on a lagoon patch reef, 1 km WSW of Carrie Bow Cay, 4 m (24 May 1975).

**REMARKS.**—The biology and living habits have been described by Davis (1966) and Fricke (1968).

#### Family OPHIOMYXIDAE

##### ***Ophiomyxa flaccida* (Say)**

*Ophiura flaccida* Say, 1825:151.

*Ophiomyxa flaccida*.—Lütken, 1859:79, 138.—Lyman, 1865:

178.—Ljungman, 1866:327.—Verrill, 1867:329; 1899a: 65; 1899b:366.—Rathbun, 1879:155.—Ives, 1889:178.—H. L. Clark, 1901:251; 1915:169; 1919:56, 71, pl. 1: figs. 1, 2; 1933:41.—Koehler, 1907:341; 1913:379; 1914:3, 132, 162.—A. H. Clark, 1921:51; 1922:210; 1939a:446; 1939b: 2; 1954:376.—Engel, 1939:4.—Fontaine, 1953:200.—Roa, 1967:282, fig. 10.—Tommasi, 1970:13, pl. 2: figs. 4, 5.—Devaney, 1974:129.—Zeiller, 1974:106 [color fig.].

MATERIAL DEPOSITED.—USNM E17759 (1 spec.); USNM E17779 (1 spec.); USNM E17780 (4 spec.); USNM E17782 (1 spec.); USNM E17857 (4 spec.).

DISTRIBUTION.—Found on the reef flat in the north *Penicillus* zone (station 4), in the coral-head/coral-pavement zone (station 6), just inside the reef crest (station 7), on the reef crest in the rubble of the coral berm (station 8), and just seaward in 0.5 m of water (station 9). Collected by bulk sample from the fore-reef slope (station 13).

REMARKS.—Taken by Devaney (1974:129) at Lighthouse Reef and Glover's Reef. As noted by H. L. Clark (1933), this species occurs along shore in very shallow water to depths below 183 m (100 fathoms).

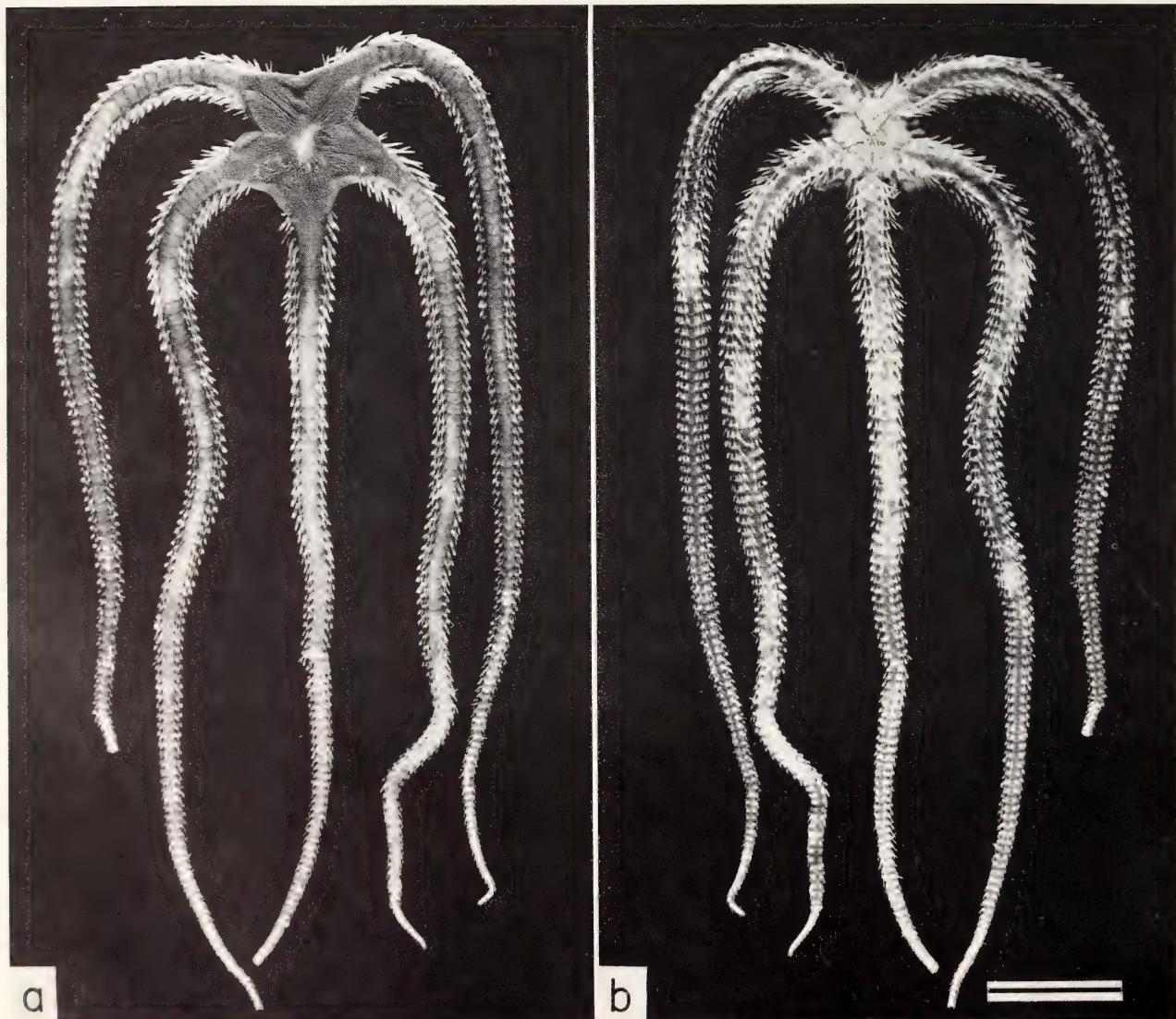


FIGURE 171.—*Ophiomitrella glabra*, USNM E17679, dry: *a*, aboral; *b*, oral. (Scale = 10 mm.)

## Family OPHIACANTHIDAE

### *Ophiomitrella glabra* (H. L. Clark)

FIGURE 171

*Ophialcea glabra* H. L. Clark, 1901:249, pl. 15: figs. 1-4.  
*Ophiomitrella glabra*.—H. L. Clark, 1915:210, 1919:56, 71; 1933:34, 43.—Parslow and Clark, 1963:26.

MATERIAL DEPOSITED.—USNM E17679 (1 spec.); USNM E17681 (1 spec.).

DISTRIBUTION.—One specimen was found on the reef crest in the rubble of the coral berm (station 8) by Kjell Sandved and one in a general sample taken from the fore-reef slope (station 13).

REMARKS.—New to Belize, the species was previously known only from the unique holotype found at Playa de Ponce, Puerto Rico.

## Family HEMIEURYALIDAE

### *Sigsbeia murrhina* Lyman

FIGURE 172

*Sigsbeia murrhina* Lyman, 1878:234, pl. 3: figs. 55, 58; 1882: 250, pl. 43: figs. 4-6; 1883:277; 1888:114, fig. 399.—Nutting, 1895:79.—Verrill, 1899a:72, pl. 2: figs. 1, 1a; 1899b:365, 381, pl. 42: fig. 7.—Koehler, 1914:133, 135, 163.—H. L. Clark, 1915:192; 1941:78.—A. H. Clark, 1921:52; 1954:376.

MATERIAL DEPOSITED.—UNSM E17682 (3 spec.).

DISTRIBUTION.—Six specimens were found in general samples from the fore-reef slope at depths from 16.0 to 27.5 m (station 13).

## Family AMPHIURIDAE

### *Amphiura fibulata* Koehler

*Amphiura fibulata* Koehler, 1913:359; 1914:2, 56, 64, 65, pl. 7: figs. 3-5.—H. L. Clark, 1915:234; 1933:35, 45.—A. H. Clark, 1954:377.—Thomas, 1962a:638, fig. 4.—Tommasi, 1965:3.

*Amphiura (Monamphiura) fibulata*.—Tommasi, 1970:45.

MATERIAL DEPOSITED.—USNM E17762 (1 spec.); USNM E17793 (1 spec.); USNM E17803 (1 spec.).



FIGURE 172.—*Sigsbeia murrhina*, USNM E17682, live. (Scale = 5 mm.)

DISTRIBUTION.—Three specimens were found among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1).

### *Amphiura stimpsonii* Lütken

*Amphiura stimpsonii* Lütken, 1859:116.—Lyman, 1865:12; 1875:4, pl. 5: fig. 66; 1882:124-143; 1883:252.—Ljungman, 1866:320; 1871:631.—Rathbun, 1879:154.—Marktanner, 1887:299.—Verrill, 1899b:376.—H. L. Clark, 1901:247; 1915:232; 1919:56, 71; 1933:35, 45.—Koehler, 1914:2, 59, 64, pl. 7: figs. 1, 2.—A. H. Clark, 1922:210; 1954:377.—Mortensen, 1936:207.—Engel, 1939:4, 7.—Fontaine, 1953:200.—Thomas, 1962a:636, fig. 3.—Parslow and Clark, 1963:43.

*Amphiura vivipara* H. L. Clark, 1918:268, pl. 1: figs. 1, 2; 1919: 56, 71.

*Monamphiura stimpsonii*.—Fell, 1962:11.

*Amphiura (Monamphiura) stimpsonii*.—Tommasi, 1970:50, pl. 24: figs. 51-52.

MATERIAL DEPOSITED.—UNSM E17763 (2 spec.); USNM E17765 (1 spec.); USNM E17775 (1 spec.); USNM E17794 (4 spec.); USNM E17796 (1 spec.); USNM E17798 (1 spec.); USNM E17801 (1 spec.); USNM E17802 (1 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); and in a general sample from the fore-reef slope (station 13).

REMARKS.—H. L. Clark (1918:268) showed that this species is viviparous.

### *Axiognathus squamatus* (Delle Chiaje)

*Ophiura elegans*.—Leach, 1815:59

*Asterias squamata* Delle Chiaje, 1829:74.

*Ophiocoma neglecta*.—Forbes, 1841:30 [text-fig.].

*Ophiolepsis squamata*.—Müller and Troschel, 1842:92.

*Amphiura squamata*.—Lyman, 1865:122; 1882:125, 136, 291, 309, 310, 314, 321, 322, 324.—Koehler, 1907:305; 1913:356.

*Amphipholis elegans*.—Ljungman, 1866:312.

*Amphipholis squamata*.—Ljungman, 1871:633.—Verrill, 1899b:312.—H. L. Clark, 1904:560, pl. 6: figs. 33, 34, pl. 7: figs. 43, 44; 1914:105, pl. 2: figs. 1–6; 1915:242. 1933:36, 50.—Coe, 1912:81, pl. 17.—Koehler, 1914:2, 52, 66, 156.—A. H. Clark, 1922:210; 1954:377.—Bernasconi, 1926:146, pl. 3.—Engel, 1939:4, 8.—Fontaine, 1953:201.—Thomas, 1962a:662, fig. 13.—Parslow and Clark, 1963:44.—Roa, 1967:286.

*Amphiura tenera* Rathbun, 1879:154.

*Axiognathus squamatus*.—Thomas, 1966:831.—Martin, 1968:65.—Tommasi, 1970:37, pl. 16: fig. 36.—Boffi, 1972:319.—Hendler, 1975:703.

MATERIAL DEPOSITED.—USNM E17764 (12 spec.); USNM E17792 (2 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1).

REMARKS.—The development of this viviparous species has been studied by numerous authors. H. L. Clark's (1933:50) statement that very young specimens may have six arms and show evidence of autotomy is probably based on Koehler's (1913:356) report of a six-armed specimen from Tortugas in which three arms are very short and in the process of regeneration; most likely

either the specimen was misidentified or it regenerated a supernumerary arm following injury. Martin (1968) and Boffi (1972) have described aspects of the ecology of this species.

### *Ophiotigma* sp.

FIGURE 173

MATERIAL DEPOSITED.—USNM E17688 (1 spec.); USNM E17689 (1 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10); and from the fore-reef slope in 26 m of water (station 13).

REMARKS.—All specimens have six rays and most show evidence of recent fissiparity. Although Koehler (1913) and H. L. Clark (1933; 1942) reported six-rayed fissiparous specimens of *Ophiotigma isacanthum*, the present material strongly suggests that the fissiparous six-rayed specimens are specifically distinct from the nonfissiparous five-rayed specimens of *O. isacanthum* and belong to an undescribed species. A. M. Clark (1967a) did not include *Ophiotigma* in her list of fissiparous ophiuroids, having previously suggested (in Parslow and Clark, 1963:37) that H. L. Clark's

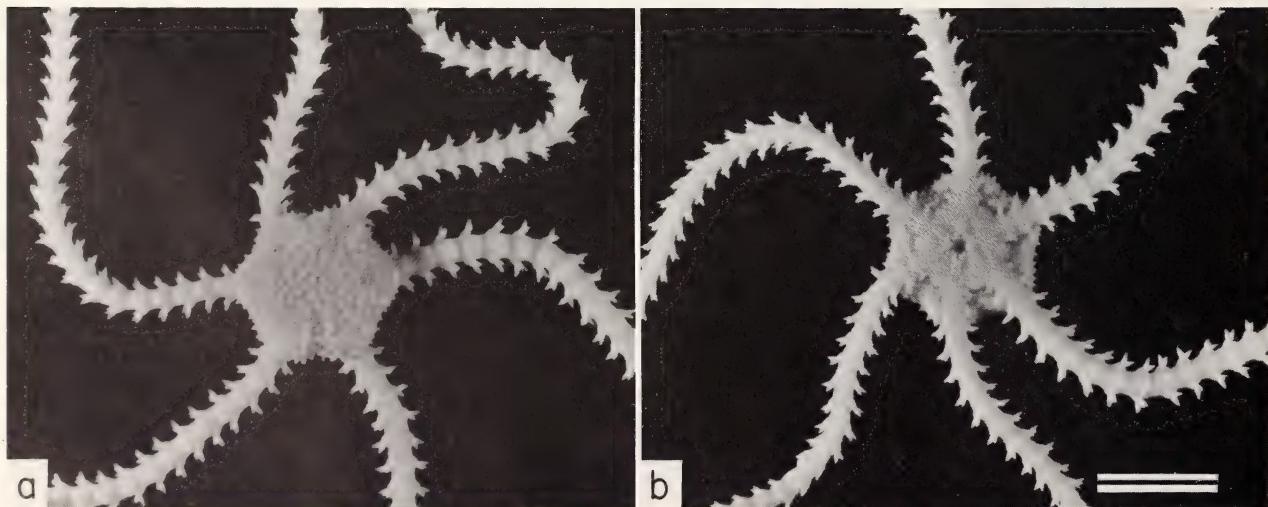


FIGURE 173.—*Ophiotigma* sp., USNM E17688, dry: a, aboral; b, oral. (Scale = 2 mm.)

(1942:377) Bermudan fissiparous specimen of *O. isacanthum* might instead be a specimen of *Ophio-comella ophiactoides*; that judgement now seems premature and calls for reexamination of the material. *Ophiotigma isacanthum* has most recently been described in detail by Thomas (1962a), but his material did not include six-rayed fissiparous specimens.

## Family OPHIACTIDAE

### *Ophioctis algicola* H. L. Clark

FIGURE 174

*Ophioctis loricata*.—H. L. Clark, 1901:246 [not Lyman, 1869: 331].

*Ophioctis plana*.—H. L. Clark, 1915:264 Bermuda [not Lyman, 1869:330].

*Ophioctis lymani*.—H. L. Clark, 1918:303, pl. 4: figs. 5, 6; 1919:57, 72.—Tommasi, 1965:5, 6; 1970:22, pl. 7: fig. 14. [Not Ljungman, 1871:629].

*Ophioctis algicola* H. L. Clark, 1933:38, 56; 1942:377.

MATERIAL DEPOSITED.—USNM E17647 (1 spec.).

DISTRIBUTION.—One specimen collected from a general bulk sample from the fore-reef slope (station 13).

REMARKS.—The species is fissiparous (H. L. Clark, 1933; but not listed by A. M. Clark, 1967a)

and this specimen has three old and three regenerating arms.

### *Ophioctis savignyi* (Müller and Troschel)

*Ophiolepis savignyi* Müller and Troschel, 1842:95.

*Ophioctis krebsii* Lütken, 1856a:12.—Lyman, 1865:111.—Verrill, 1868:366; 1899b:376.—Ljungman, 1871:627.—Rathbun, 1879:153.—H. L. Clark, 1901:246.

*Ophioctis virescens* Lütken, 1856a:24.

*Ophiolepis sexradia* Grube, 1857:343.

*Ophioctis reinhardtii* Lütken, 1859:161, pl. 3: fig. 7a,b.

*Ophioctis savignyi*.—Ljungman, 1866:323.—Koehler, 1907: 311; 1913:351; 1914:2, 41, 154.—H. L. Clark, 1914:96, pl. 1: figs. 1-19, pl. 3: figs. 12-14; 1915:265; 1918:305; 1919: 57, 72; 1933:38, 59; 1942:377.—A. H. Clark, 1921:53; 1922:211; 1939a:447, 1939b:3; 1954:377.—Engel, 1939:4, 8.—Fontaine, 1953:201.—John and Clark, 1954:140.—Roa, 1967:288.—Tommasi, 1970:24, pl. 8: figs. 16, 17.—Boffi, 1972:319.—Devaney, 1974:129.—Pawson, 1978:11.

*Ophioctis incisa* von Martens, 1870:248.

*Ophioctis brocki* de Loriol, 1893:401.

MATERIAL DEPOSITED.—USNM E17732 (2 spec.); USNM E17797 (1 spec.); USNM E17804 (1 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); on the reef flat in the south *Penicillus* zone (station 5); in the coral-head/coral-pavement zone (station 6); in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of

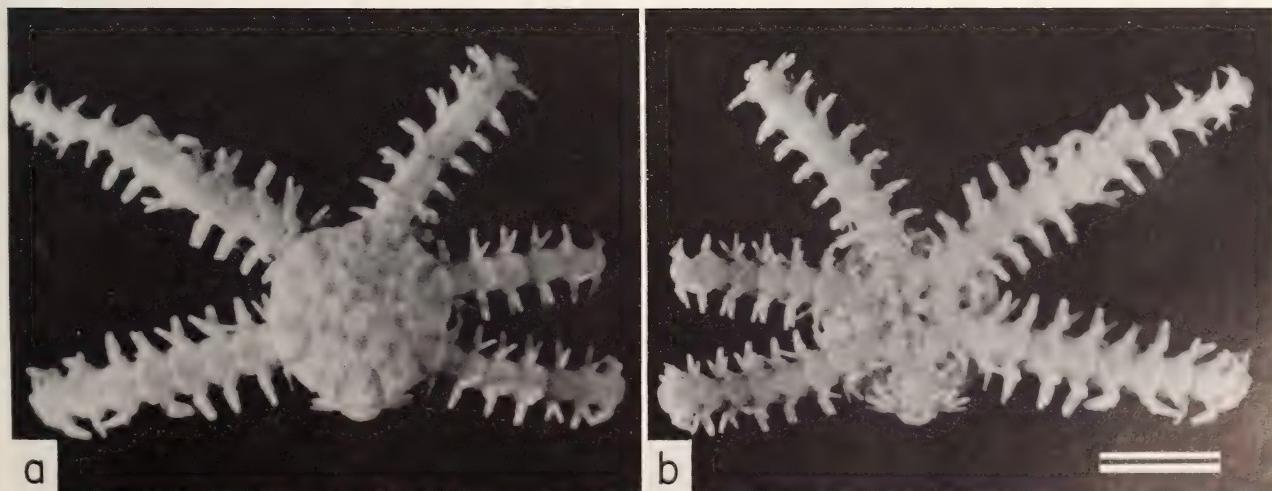


FIGURE 174.—*Ophioctis algicola*, USNM E17647, dry: a, aboral; b, oral. (Scale = 1 mm.)

water (station 10); from the sponge *Siphonodictyon coralliphagum* Rützler at 24 m in the sand trough of the outer fore reef (station 11), and from the fore-reef slope in 26 m of water (station 13).

**REMARKS.**—Two specimens from the fore-reef slope are five armed with the primary rosette perfectly intact, indicating that they never underwent autotomous fission. The relation of old to new arms in most specimens is 6 plus 0 or 3 plus 3, but one from the lagoon has the relation 2 plus 3. Previously reported from Glover's Reef (Devaney, 1974:129).

### Family OPHIOTRICHIDAE

#### *Ophiothrix (Acanthophiothrix) suensonii* Lütken

*Ophiothrix suensonii* Lütken, 1856a:16; 1859:250, pl. 4: fig. 2a-e.—Lyman, 1865:157; 1882:215, 218, 222, 223, 229, 312, 315, 326.—Rathbun, 1879:153.—Ives, 1889:178.—Verrill, 1899a:21; 1899b:375.—H. L. Clark, 1901:244; 1915:279; 1918:313; 1919:57, 72; 1933:38, 62.—Koehler, 1907:388; 1913:376; 1914:3, 121, 161.—A. H. Clark, 1921:54; 1922:211; 1939a:447; 1954:377.—Boone, 1933:111, pl. 64.—Engel, 1939:4.

*Ophiothrix suensonii*.—Ljungman, 1866:331; 1871:627.—Parslow and Clark, 1963:45.—Roa, 1967:289.—Tommasi, 1971:7, figs. 21c, 22c, 23c.

*Ophiothrix (Acanthophiothrix) suensonii*.—A. M. Clark, 1967b: 638, 643, 648, fig. 1j.—Tommasi, 1970:62.—Devaney, 1974:130.

**MATERIAL DEPOSITED.**—USNM E17734 (2 spec.); USNM E17787 (1 spec.); USNM E17808 (1 spec.); USNM E17850 (2 spec.).

**DISTRIBUTION.**—Collected in the spur and groove zone of the inner fore reef from a coral bulk sample in 10 to 12 m of water (station 10), and in 24 m in the outer fore reef near the bottom of a trough among, and in crevices of, coral clumps (station 11).

**REMARKS.**—Previously recorded from Belize (Koehler, 1914:122), Turneffe Islands, Lighthouse Reef, and Glover's Reef (Devaney, 1974:130).

#### *Ophiothrix (Ophiothrix) angulata* (Say)

*Ophiura angulata* Say, 1825:145.

*Ophiothrix angulata*.—Ayres, 1852:249.—Lütken, 1859:219.—

Lyman, 1865:3, pl. 2: figs. 1-3; 1882:214, 216, 218, 219, 286, 287, 290, 312, 325.—Ljungman, 1866:331.—Ludwig, 1882:18.—Ives, 1889:178; 1890:332.—Verrill, 1899a:18; 1899b:375.—H. L. Clark, 1901:244; 1914:111, pl. 2: figs. 7-12, pl. 3: figs. 1-10, 15-19; 1915:269; 1918:312; 1919:57, 72; 1933:38, 60; 1941:86.—Koehler, 1907:330; 1913:375; 1914:3, 118, 160.—A. H. Clark, 1921:53; 1922:211; 1939a:447; 1954:377.—Boone, 1933:110.—Engel, 1939:4, 8.—Fontaine, 1953:202.—Tabb and Manning, 1961:566.—Parslow and Clark, 1963:45.—Roa, 1967:289.—Tommasi, 1971:7, figs. 21b, 22b, 23b.—Boffi, 1972:319.—Godcharles and Jaap, 1973:57.

*Ophiothrix violacea* Müller and Troschel, 1842:115.—Lütken, 1859, pl. 4: fig. 1a-g.—Verrill, 1868:366.—Rathbun, 1879:152.—Koehler, 1907:339.

*Ophiothrix (Ophiothrix) angulata*.—A. M. Clark, 1967b:646.—Tommasi, 1970:54.—Devaney, 1974:130.

**MATERIAL DEPOSITED.**—USNM E17805 (3 spec.); USNM E17809 (1 spec.); USNM E17846 (5 spec.).

**DISTRIBUTION.**—Found among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); on the reef flat in the south *Penicillllus* zone among crevices of rocks and shells (station 5); in the spur and groove zone of the inner fore reef from a coral bulk sample in 10 to 12 m of water (station 10); from the outer ridge of the outer fore reef (station 12); and from the fore-reef slope to approximately 28 m (station 13).

**REMARKS.**—Previously recorded from Belize (Koehler, 1914:122) and from the Turneffe Islands, Lighthouse Reef, and Glover's Reef (Devaney, 1974:130). Shades of green and brown in life have turned blue in many of the preserved specimens.

#### *Ophiothrix (Ophiothrix) lineata* Lyman

*Ophiothrix lineata* Lyman, 1860:201.—Ives, 1889:178.—Verrill, 1899b:375.—Koehler, 1907:334, pl. 13: figs. 46, 47; 1913:376; 1914:3, 120, 161.—H. L. Clark, 1915:273; 1918:315; 1919:57, 72; 1933:38, 62.—A. H. Clark, 1922:211; 1954:377.—Engel, 1939:4.—Tommasi, 1970:54.

*Ophiothrix (Ophiothrix) lineata*.—A. M. Clark, 1967b:647.—Devaney, 1974:131.

Not *Ophiothrix lineata*.—A. H. Clark, 1921:54, reidentified in A. H. Clark, 1939a:449, as *Ophiothrix platyactis* H. L. Clark, 1939.

**MATERIAL DEPOSITED.**—USNM E17761 (1 spec.).

**REMARKS.**—One specimen was found in the temporary aquaria on Carrie Bow Cay. Previously reported from Turneffe Islands (Devaney, 1974:131).

### *Ophiothrix (Ophiothrix) oerstedi* Lütken

*Ophiothrix oerstedi* Lütken, 1856a:15; 1859:149, pl. 4: fig. 3a-e.—Ljungman, 1866:331; 1871:626.—Ives, 1889:178; 1891:340.—Stearns, 1891:4.—Verrill, 1899a:20; 1899b:375.—H. L. Clark, 1901:244; 1915:276; 1918:313, 314; 1919:57, 72, pl. 2; 1933:38, 63.—Koehler, 1907:336; 1913:376; 1914:3, 121, 161.—A. H. Clark, 1921:54; 1922:211; 1939a:447; 1939b:3; 1954:377.—Engel, 1939:4, 8.—Roa, 1967:290.—Tommasi, 1970:53. [Includes the spellings *oerstedi*, *oerstedi*, and *orstedii*.]

*Ophiothrix (Ophiothrix) oerstedi*.—A. M. Clark, 1967b:647.—Devaney, 1974:131.

**MATERIAL DEPOSITED.**—USNM E17739 (1 spec.); USNM E17843 (1 spec.); UNSM E17844 (1 spec.); USNM E17849 (1 spec.).

**DISTRIBUTION.**—This species was widely taken. Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); under rocks in a rubble area between sand and *Thalassia* on the lagoon side of the south end of Carrie Bow Cay (station 2); on the reef flat in the coral-head/coral-pavement zone (station 6); just inside the reef crest (station 7); on the reef crest in the rubble of the coral berm (station 8); in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10), and in 15 to 28 m on the fore-reef slope (station 13).

**REMARKS.**—Previously reported from Light-house Reef and Glover's Reef (Devaney, 1974: 131). Shades of brown in life have turned blue in the preserved specimens.

## Family OPHIONEREIDAE

### *Ophionereis reticulata* (Say)

*Ophiura reticulata* Say, 1825:148.

*Ophiolepis nereis* Lütken, 1856a:11; 1856b:24.

*Ophionereis reticulata*.—Lütken, 1859:212, pl. 3: fig. 6a-c.—Lyman, 1865:141; 1875:4; 1878:224; 1882:162, pl. 40: figs. 13-15; 1883:253.—Ljungman, 1866:310; 1871:620.—Verrill, 1867:342; 1868:366; 1899a:30; 1899b:377.—Rathbun, 1879:152.—Ives, 1889:177.—Lütken and Mortensen, 1899:162, pl. 13: fig. 10.—H. L. Clark, 1901:249; 1915:

289; 1919:57, 58, 72; 1933:39, 64; 1942:378.—Koehler, 1907:315; 1913:360; 1914:2, 44, 59, 155.—A. H. Clark, 1921:42, 55; 1922:211; 1939a:450; 1954:377.—Engel, 1939:5, 8.—Fontaine, 1953:202.—A. M. Clark, 1953:67, 68, 73, fig. 3a, pl. 1: figs. 1, 2.—Millott, 1953:96-99.—Brito, 1960:2, fig. 2.—Tabb and Manning, 1961:566.—Parslow and Clark, 1963:27, 47.—Tommasi, 1970:86, 88, pl. 40: figs. 92, 93.—Boffi, 1972:319.—Godcharles and Japp, 1973:57.—Thomas, 1973:586, figs. 1, 5a.—Devaney, 1974:132.

*Amphiura steamsi* Ives, 1891:339, 340, pl. 16: figs. 1-3.

*Ophionereis olivacea*.—Roa, 1967:284, fig. 12 [not *O. olivacea* H. L. Clark, 1901].

**MATERIAL DEPOSITED.**—USNM E17738 (1 spec.); USNM E17851 (2 spec.).

**DISTRIBUTION.**—Collected in the lagoon at the south end of South Water Cay and from the pile of discarded conch shells at the foot of the pier of Carrie Bow Cay (station 1); on the reef flat in both the north and south *Penicillus* zone (stations 4 and 5); and from just inside the reef crest (station 7). Two juvenile specimens were collected by bulk sample from the fore-reef slope (station 13).

**REMARKS.**—Previously reported from Light-house Reef (Devaney, 1974:132).

### *Ophionereis squamulosa* Koehler

FIGURE 175

*Ophionereis dubia*.—H. L. Clark, 1901:248 [not *O. dubia* Müller and Troschel, 1842].

*Ophionereis squamata*.—Koehler, 1913:360, pl. 21: figs. 4-6 [not *O. squamata* Ljungman, 1866:310].

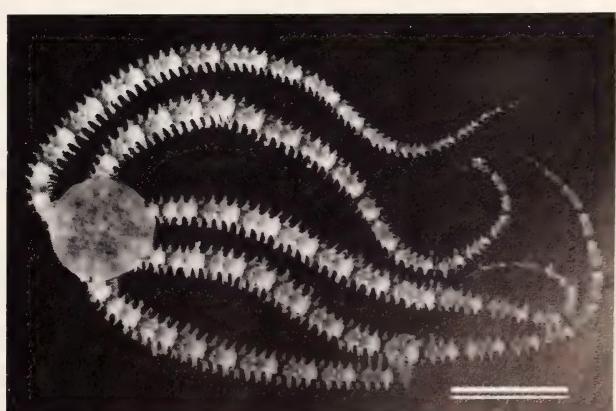


FIGURE 175.—*Ophionereis squamulosa*, USNM E17847, live. (Scale = 5 mm).

*Ophionereis squamulosa* Koehler, 1914:2, 44.—H. L. Clark, 1915:290; 1918:326; 1919:57, 58, 59, 72; 1933:39, 65.—Mortensen, 1921:171–177, pl. 31: figs. 1–6.—Pearson, 1936:70–72 [possibly *O. reticulata*].—A. H. Clark, 1939a: 450.—A. M. Clark, 1953:67, 71, fig. 2, pl. 3: figs. 3, 4.—Parslow and Clark, 1963:27, 47.—Tommasi, 1970:87, 88, pl. 41: fig. 94.—Thomas, 1973:588, figs. 2, 5b.

*Ophionereis reticulata*.—Roa, 1967:284 [probably *O. squamulosa*].

MATERIAL DEPOSITED.—USNM E17847 (1 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); on the reef flat in the coral head/coral pavement zone (station 6); and from the spur and groove zone of the inner fore reef in 10 to 12 m of water (station 10).

#### Family OPHIOCOMIDAE

##### *Ophiocoma echinata* (Lamarck)

*Ophiura echinata* Lamarck, 1816:543.

*Ophiocoma echinata*.—Agassiz, 1835:192.—Lütken, 1859:244, pl. 4: fig. 7a–d.—Lyman, 1865:81.—Ljungman, 1871: 621.—Rathbun, 1879:152.—Ives, 1889:177.—Grave, 1898:6, figs. 1–6.—Verrill, 1899a:22; 1899b:375.—H. L. Clark, 1901:245; 1915:291; 1919:57, 72; 1921:125; 1933: 39, 65; 1941:89.—Koehler, 1907:325; 1913:374; 1914:3, 117, 159.—A. H. Clark, 1921:55; 1922:212; 1939a:450, pl. 54: fig. 4; 1954:377.—Engel, 1939:5, 8.—Fontaine, 1953: 199, 203.—John and Clark, 1954:140.—Parslow and Clark, 1963:46.—Roa, 1967:292.—Tommasi, 1970:81.—Devaney, 1974:132.—Zeiller, 1974:107 [color fig.].

*Ophiocoma crassispina* Say, 1825:147.—Ljungman, 1866: 329.—Ives, 1889:177.

MATERIAL DEPOSITED.—USNM E17845 (1 spec.); USNM E17854 (3 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); under rocks in a rubble area between sand and *Thalassia* on the lagoon side of the south end of Carrie Bow Cay (station 2); in the patch reef zone of the back reef along the transect (station 3); on the reef flat in both the north and south *Penicillus* zone (stations 4 and 5); among coral rubble in the coral-head/coral-pavement zone (station 6); just inside the reef crest (station 7); on the reef crest in the rubble of the coral berm (station 8); and in the

spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10).

REMARKS.—Very common. Previously reported from Lighthouse Reef and Glover's Reef (Devaney, 1974:132).

##### *Ophiocoma paucigranulata* Devaney

*Ophiocoma paucigranulata* Devaney, 1974:132, figs. 5–8.

MATERIAL DEPOSITED.—USNM E17783 (19 spec.); USNM E17784 (1 spec.); USNM E17785 (1 spec.); USNM E17786 (3 spec.).

DISTRIBUTION.—Twenty-five specimens collected on the reef crest in the rubble of the coral berm (station 8), and one specimen taken by bulk sample from the outer ridge of the outer fore reef (station 12).

REMARKS.—Devaney (1974:132) described this species on the basis of two specimens from Long Cay, Lighthouse Reef. Our specimens have the disc thoroughly covered with granules but otherwise they agree with Devaney's description.

##### *Ophiocoma pumila* Lütken

*Ophiocoma pumila* Lütken, 1859:141, 146, pl. 4: fig. 5a–c [not 1859:248, pl. 4: fig. 5d, = *Ophiocomella ophiactoides* (H. L. Clark)].—Lyman, 1865:71.—Ljungman, 1866:328; 1871: 621.—Ives, 1889:177.—Verrill, 1899a:23; 1899b:375.—H. L. Clark, 1901:245; 1915:293; 1919:57, 72; 1921:131; 1933:39, 67.—Koehler, 1907:326; 1913:375; 1914:3, 117, 160.—A. H. Clark, 1921:55; 1922:212; 1939a:451 [not pl. 54: fig. 3 = *Ophiocomella ophiactoides*]; 1954:377.—Engel, 1939:5, 9.—Fontaine, 1953:199, 203.—Roa, 1967:292, fig. 22.—Tommasi, 1970:82.—Devaney, 1970:10, 28, 29, 30–32, fig. 16; 1974:139.

MATERIAL DEPOSITED.—USNM E17799 (2 spec.); USNM E17807 (3 spec.); USNM E17853 (1 spec.).

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); on the reef flat under coral rubble in the coral-head/coral-pavement zone (station 6); just inside the reef crest (station 7); on the reef crest in the rubble of the coral berm (station 8); in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10),

and in about 26 m of water on the fore-reef slope (station 13).

**REMARKS.**—Common. One specimen from station 1 has six arms and shows no evidence of fissiparity; it is not *Ophiocomella ophiactoides*. Previously reported from Belize (Koehler, 1914:160) and from Turneffe Islands, Lighthouse Reef, and Glover's Reef (Devaney, 1974:139).

### *Ophiocoma wendti* Müller and Troschel

*Ophiocoma wendti* Müller and Troschel, 1842:99.—Ljungman, 1871:621.—Devaney, 1970:34, 35, 37; 1974:140.

*Ophiocoma riisei* Lütken, 1859:243, 245, pl. 4; fig. 6a-d.—Lyman, 1865:76.—Ljungman, 1866:328.—Rathbun, 1879:152.—Ives, 1889:177.—Stearns, 1891:4.—Verrill, 1899a:22; 1899b:375.—H. L. Clark, 1901:245; 1915:293; 1919:57, 72; 1921:128; 1933:39, 66.—Koehler, 1907:326; 1913:375; 1914:3, 118, 159.—A. H. Clark, 1921:56; 1922:212; 1939a:450, pl. 54: fig. 5; 1954:377.—Engel, 1939:5.—Fontaine, 1953:199, 203.—Parslow and Clark, 1963:47.—Roa, 1967:292.—Tommasi, 1970:82.

Not *Ophiocoma wendti*.—Koehler, 1907:327, pl. 13: fig. 38.—H. L. Clark, 1921:129.

**MATERIAL DEPOSITED.**—USNM E17733 (1 spec.); USNM E17737 (1 spec.); USNM E17855 (2 spec.).

**DISTRIBUTION.**—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); on the reef flat in the north and south *Penicillus* zones (stations 4 and 5); under coral rubble in the coral-head/coral-pavement zone (station 6); on the reef crest in the rubble of the coral berm (station 8); in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10); and by bulk sample from the outer ridge of the outer fore reef (station 12).

**REMARKS.**—Common. Previously reported from Belize (Koehler, 1914:159, as *O. riisei* Lütken) and from Lighthouse Reef and Glover's Reef (Devaney, 1974:140).

### *Ophiocomella ophiactoides* (H. L. Clark)

*Ophiocoma pumila* [part] Lütken, 1859:248, pl. 4: fig. 5d [not 1859:141, 146, pl. 4: fig. 5a-c].—A. H. Clark, 1922:212; 1939a:451, pl. 54: fig. 3.—H. L. Clark, 1942:378 [questionable].

*Ophiacantha ophiactoides* H. L. Clark, 1901:249, pl. 15: figs. 5-8; 1915:207; 1933:34, 43.

*Ophiacantha oligacantha* H. L. Clark, 1918:265-267, pl. 7: fig. 5; 1919:56, 71.

*Ophiocomella caribbaea* A. H. Clark, 1939b:7-8.

*Ophiocomella ophiactoides*.—A. M. Clark in Parslow and Clark, 1963:37, fig. 11; 1967:151.—Roa, 1967:291, fig. 21.

**MATERIAL DEPOSITED.**—USNM E17736 (1 spec.).

**DISTRIBUTION.**—Collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1); on the reef flat in the south *Penicillus* zone (station 5); and in the coral-head/coral-pavement zone (station 6).

**REMARKS.**—Five specimens have recently autotomized and have three arms and a broken disc. Of these, one is 2+1+0 and one is 1+2+0 (old to regenerating to new arms). Of the other specimens, one has five arms and shows no evidence of fissiparity; fourteen have six arms, showing three old and three regenerating arms when the distinction can be made, and two of these can be further categorized as 2+1+3; one has six arms with two old and four regenerating arms; and one has seven arms with four old and three regenerating arms.

### *Ophiopsila riisei* Lütken

FIGURE 176

*Ophiopsila riisei* Lütken 1859:136, pl. 5: fig. 2a-c.—Lyman, 1865:150, figs. 16-17.—Ljungman, 1866:330; 1871:621.—Rathbun, 1879:152.—Verrill, 1899a:23.—H. L. Clark, 1901:245; 1915:299; 1918:330; 1919:57, 72; 1933:39, 67.—Koehler, 1907:315; 1914:2, 45, 155.—A. H. Clark, 1939a:452; 1954:377.—Roa, 1967:293.—Tommasi, 1970:85.

**MATERIAL DEPOSITED.**—USNM E17648 (2 spec.); USNM E17758 (7 spec.); USNM E17790 (1 spec.).

**DISTRIBUTION.**—Twelve specimens from coral substrate from the fore-reef slope (station 13).

**REMARKS.**—One specimen has an amphiurid clinging mouth to mouth. Three arms of the amphiurid are extended in the gutter formed by the lowermost *Ophiopsila* arm spines (Figure 176). Without separating the organisms, identification of the amphiurid as cf. *Amphiura stimpsoni* is only tentative.

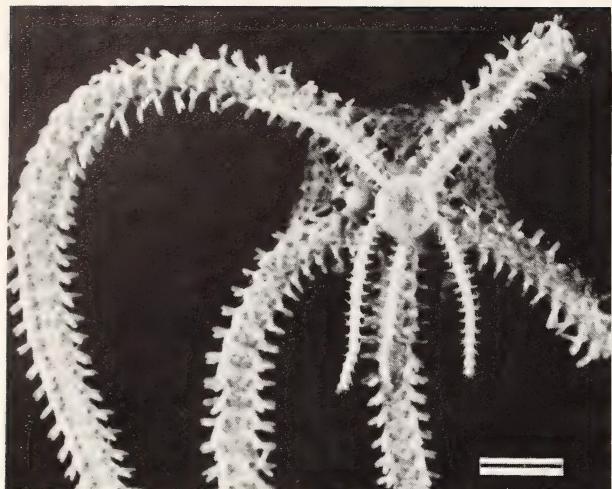


FIGURE 176.—*Ophiopsila riisei*, with small amphipod cf. *Amphiura stimpsonii* clinging mouth to mouth; USNM E17648, dry. (Scale = 2 mm.)

### Family OPHIODERMATIDAE

#### *Ophioderma anitae* new species

FIGURES 177, 178a; PLATE 5: top right

MATERIAL DEPOSITED.—Nine specimens collected on the reef crest in the rubble of the coral berm (station 8) on 3, 5, and 7 May 1974.

*Holotype*: USNM E17641, 5 May 1974 (photographed).

*Paratypes*: USNM E17642 (1 spec., photographed), USNM E17643 (1 spec.); USNM E17644 (2 spec.), USNM E17645 (3 spec.), all 3 May 1974; USNM E17646 (1 spec.), 7 May 1974.

DIAGNOSIS.—Upper arm plates composed of a single piece, not fragmented; proximal upper arm plates nearly twice as broad as long, broadly in contact, with slight concave arc to distal edge. Disc granules fine, closely spaced, not squamose. Oral and adoral shields and small radial shields not covered by granules. Arms long, up to five and two-thirds times disc diameter, uniformly tapering, circular in section proximally, flat in section near the tip, exceedingly smooth where arm spines are pressed in. Arm spines 7 to 9, rarely 10. Disc grayish brown with yellow splotches, white underside; arms brown above, buff below, yellow-brown arm spines.

DESCRIPTION.—*Holotype*: Disc diameter 18.4 mm. Arm length from edge of disk 104.6 mm.

The disc is about circular with slight interradial swellings. It is covered on both surfaces with very fine granules that are closely spaced but not touching, and that on the upper surface leave only the radial shields exposed. The radial shields are very small and only measure about 1.2 mm in length; they are irregularly oval, about two-thirds as broad as long. The two shields of each pair are separated by a space about as wide as the width of the arm base. The granules of the upper surface of the disc do not pass out onto the upper surface of the arms or onto the few disc scales that form short radial notches, which encompass two minute upper arm plates, a half-exposed upper arm plate and an almost fully exposed upper arm plate.

The under surface of the disc is covered with granules identical with those of the upper surface, but the oral and adoral shields and the scales between the outer genital slits and the arm bases are free of granules. The inner genital slits extend from near the distal edge of the first side arm plate to one or less granules short of the oral shields. The outer genital slits are located approximately at the level of the fifth side arm plate and are bordered on their interradial edge by 14 to 16 granules.

The oral shields are large, almost five-sided, not quite twice as wide as high; the distal border is almost straight or slightly concave except in the madreporic interradius where it is slightly convex; the proximal corner is broadly rounded and confluent with the adjoining sides, and at its tips there is a small to minute supplementary plate without granules. The adoral shields form broad lobes at the radial corners of the oral shields and adjoin the outermost oral papillae, the lower edge of the buccal tentacle scale and the lateral corners of the first (zeroeth in terms of visible arm segments) ventral arm plate; they are separated by granules from the first side arm plates. The oral plates are concealed by granules. Not counting the buccal tentacle, there are nine oral papillae on the side of most jaw angles, but sometimes eight or 10. The outermost are broadest, about as

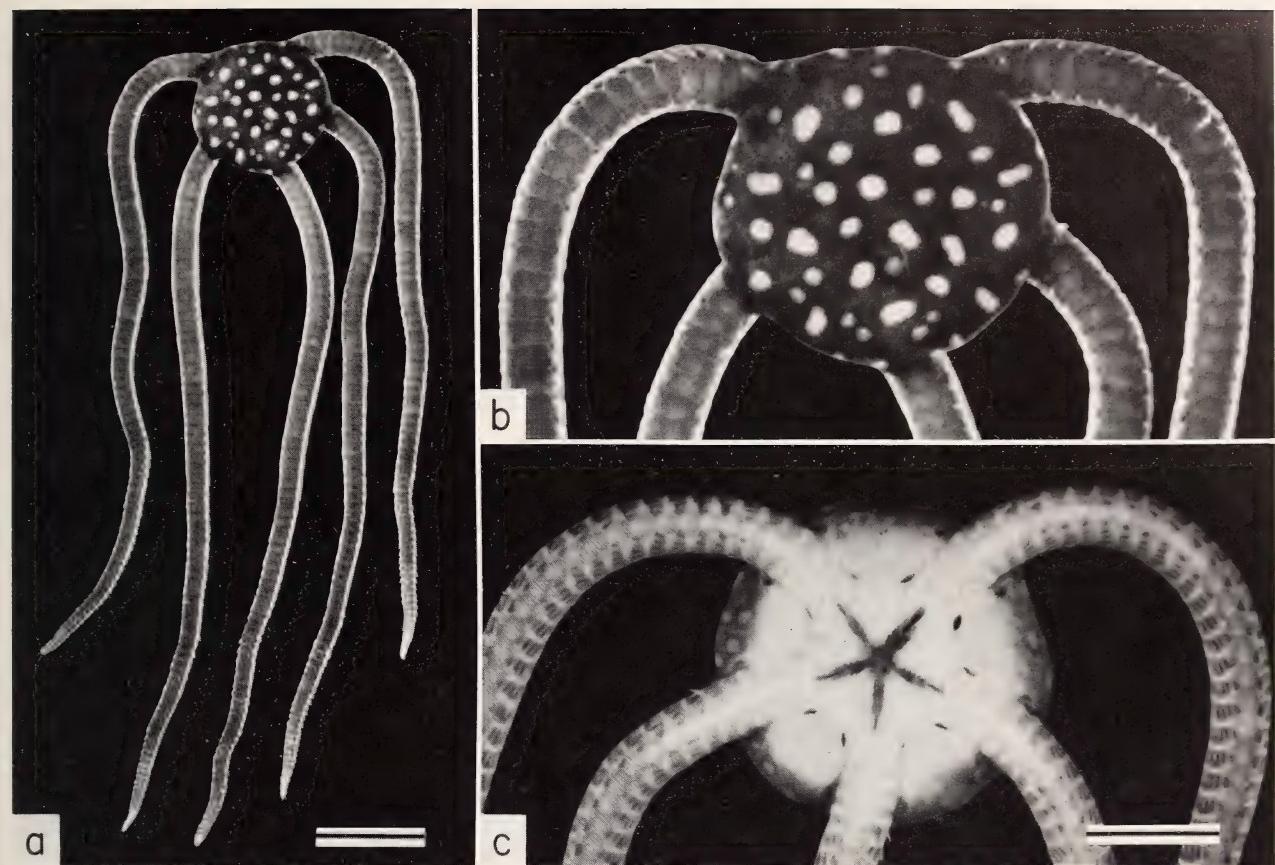


FIGURE 177.—*Ophioderma anitae*, USNM E17641, holotype, live: *a*, *b*, aboral; *c*, oral. (Scale = 10 mm for *a*; 5 mm for *b*, *c*.)

broad as long; the others are somewhat prism shaped, about twice as long as broad, becoming more pointed toward the apex of the jaw, overlapping in the direction of the jaw apex; the two at the apex of the jaw are again quite large and overlie the vertical row of teeth.

The arms are circular in section proximally, long, and very slightly and uniformly tapering in both width and thickness, gradually becoming very flat in section near the arm tip; exceedingly smooth where arm spines are pressed against the side of the arms.

Upper arm plates composed of a single piece, not fragmented. The upper arm plates beyond the radial notch are very wide, nearly rectangular but having a subtle yet distinct concave arc to the distal edge, changing to a similarly subtle convex arc which strengthens near the uppermost

arm spine. Viewed from above, the proximal upper arm plates are slightly more than twice as wide as long. Near the arm tips the plates become trapezoidal, about as wide as long, as the side arm plates encroach on the upper surface of the arm. The upper arm plates are broadly in contact except for the last 10 or so segments at the arm tip.

The first lower arm plate, not associated with a visible arm segment, is about twice as broad as long; the distal edge is shallowly rounded or very slightly angular. Between this and the lower arm plate of the first arm segment there is a pair of narrow slit-like, almost concealed, pores. There are no such pores between succeeding lower arm plates. The succeeding lower arm plates overlap slightly and appear nearly circular proximally, rounded-octagonal more distally, owing in part

to strong overlap by the inner tentacle scales; close to the tip of the arm they ultimately become fan shaped as the side arm plates encroach further onto the under surface of the arm.

The side arm plates abut in smooth contour the upper and lower arm plates, giving the arm its very smooth nearly circular section. The arm spines also match this contour when pressed against the side of the arm. The arm spines are therefore flat; they gradually increase in length from uppermost to lowermost, and taper to a blunt tip. Length of uppermost arm spines about half an arm segment long, overlapping and often extending beyond the rounded lower edge of the upper arm plate. Lowermost arm spines slightly overlap succeeding tentacle scales, with greater overlap on the first seven arm segments. The number of arm spines by segment are given in Table 28.

Two tentacle scales are present except at the very tip of the arm where only one is seen. Outer tentacle scale substantially wider than inner, squarish, resembling a ninety degree quadrant of a circle, and overlapping the articular base of the lowermost arm spine. Inner tentacle scale approximately oval, about two and one-half to three times as long as broad, about half an arm segment long, and about one-half to one-third again as long as the outer tentacle scale. The distance between the inner edges of the inner tentacle scales of two sides of an arm is about one and

one-half to one and two-thirds the length of one inner tentacle scale (Figure 178a).

Coloration, grayish brown with yellow splotches, is shown in Plate 5 (top right). In alcohol yellow areas have turned white, and the brown has dulled on drying. The yellow splotches vary from nearly circular to oval and are somewhat smaller than the radial shields. Radial shields are the same brown as the ground color of the disc; however, the disc scales beneath the brown granules are only tinged with brown in the preserved specimen. Side arm plates are brown, under surface of disc white, under arm plates buff, and arm spines yellow-brown. There are no banding patterns on the arms.

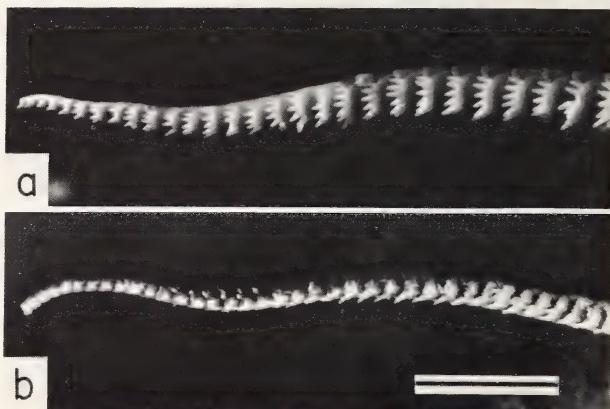


FIGURE 178.—Comparison of arm tips in two species of *Ophioderma*: a, *O. anitae*, USNM E17645, dry; b, *O. rubicundum*, USNM E17683, dry. (Scale = 5 mm.)

TABLE 28.—Number of arm spines by segments in specimens of *Ophioderma anitae*, new species

Specimen	Segment number																									Disc diameter (mm)	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
HOLOTYPE																											18.5
USNM E17641	3	4	5	6	7	7	9	9	9	9	10	9	8	9	9	9	9	9	9	9	9	9	9	9	8	18.5	
PARATYPES																											
USNM E17646	3	3	5	6	7	7	8	9	9	9	9	9	9	8	9	9	8	8	8	8	7	8	8	8	8	17.3	
USNM E17644	2	3	4	5	6	7	8	8	8	8	8	8	8	8	8	8	8	7	8	7	7	7	7	7	7	17.0	
USNM E17645	2	3	4	5	6	6	7	9	9	9	9	9	9	8	9	9	10	9	9	9	8	8	8	9	8	16.3	
USNM E17645	3	3	4	5	6	7	8	9	9	9	9	9	9	9	9	9	9	9	9	9	9	8	9	8	9	14.0	
USNM E17645	3	4	5	6	7	8	9	8	9	9	8	9	8	9	8	8	8	8	8	8	8	8	8	8	8	13.7	
USNM E17643	2	4	4	5	6	7	8	7	7	8	7	9	8	8	8	8	8	9	8	8	8	8	8	8	8	13.5	
USNM E17644	3	3	5	5	6	7	8	8	8	8	7	8	8	8	8	8	8	8	8	8	8	8	8	8	8	12.0	
USNM E17642	2	4	4	5	6	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6	7	7	11.3	

*Paratypes*: Disc diameters range from 11.3 to 17.3 mm. In the smaller specimens the arms are disproportionately shorter, the outer genital slit is beside the fourth side arm plate, there can be only seven or eight oral papillae, the yellow markings are more commonly larger than the radial shields, often there is no evidence of a supplementary plate at the proximal corner of the oral shield, and the oral shields are more nearly as wide as high.

**COMPARISON WITH OTHER SPECIES.**—*Ophioderma anitae* keys to the *O. cinereum*, *O. phoenium*, and *O. rubicundum* couplets of H. L. Clark's (1933) key, and to the *O. pallidum* (Verrill)—*O. phoenium* couplet in Ziesenhenne's (1955) key. *Ophioderma cinereum* is distinguished from the present species by its subdivided upper arm plates; *O. phoenium* is recognized by adoral shields covered with granules; *O. rubicundum* is closest but is entirely different in color and details of morphology. In a specimen of *O. rubicundum* from the same habitat (USNM E17683) with disc diameter 14.8 mm the length of the first 15 segments from the mouth frame is 14.5 mm, whereas in a specimen of *O. anitae* (USNM E17645) with disc diameter 14.0 mm the length of the first 15 segments from the mouth frame is 15.3 mm (Figure 178). Further, the arm tips of *O. rubicundum* are more slender and not as flattened as in *O. anitae* (Figure 178).

**ETYMOLOGY.**—Named for Anita Pruzan.

### *Ophioderma appressum* (Say)

PLATE 5: top right

*Ophiura appressa* Say, 1825:151.—Lyman, 1865:34.—Rathbun, 1879:151.—Ives 1889:175.—Verrill, 1899a:6.—H. L. Clark, 1901:242.—A. H. Clark, 1939b:10.

*Ophioderma virescens* Lütken, 1859:86, pl. 1: fig. 4a-d.

*Ophioderma appressum*.—Ljungman, 1866:304; 1871:615.—Lyman, 1882:9.—Koehler, 1913:353.—H. L. Clark, 1915:300; 1919:57, 72; 1933:40, 68; 1942:379.—A. H. Clark, 1922:213; 1939a:452; 1954:377.—Boone, 1933:113, pls. 66, 75b, 76b.—Engel, 1939:5, 9.—Caso, 1951:219, 222, 243, 249, 254, figs. 15-18; 1953:222.—Ziesenhenne, 1955:188, 200.—Costa and Costa, 1962:3.—Parslow and Clark, 1963:47.—Roa, 1967:294.—Boffi, 1972:319.—Devaney, 1974:141, fig. 9.—Zeiller, 1974:107 [color fig.].

*Ophioderma appressa*.—Koehler, 1907:281; 1914:1, 3, 147.—A.

H. Clark, 1921:56; 1939b:10.—Caso, 1961:176-178, figs. 74, 75.—Tommasi, 1970:65.

**MATERIAL DEPOSITED.**—USNM E17676 (3 spec.); USNM E17678 (2 spec.); USNM E17680 (2 spec.).

**DISTRIBUTION.**—Two specimens collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1). Very common on the reef flat where it was collected in the north and south *Penicillus* zones (stations 4 and 5), and in the coral-head/coral-pavement zone (station 6). Collected just inside the reef crest (station 7) and on the reef crest in the rubble of the coral berm (station 8).

**REMARKS.**—Previously reported from Light-house Reef and Glover's Reef (Devaney, 1974: 141).

### *Ophioderma brevicaudum* Lütken

*Ophioderma brevicaudum* Lütken, 1856a:8; 1859:94, pls. 1, 2: fig. 3a-c.—H. L. Clark, 1915:300; 1919:57, 72; 1933:40, 69.—A. H. Clark, 1922:213; 1939a:452, pl. 54: figs. 1, 2; 1954:377.—Engel, 1939:5, 9.—John and Clark, 1954: 140.—Ziesenhenne, 1955:188, 199.—Roa, 1967:294.—Devaney, 1974:141.

*Ophiura brevicauda*.—Verrill, 1899a:5.—H. L. Clark, 1901: 242.

*Ophioderma brevicauda*.—Ljungman, 1866:303; 1871:615.—Koehler, 1907:281; 1914:1, 4, 147.—A. H. Clark, 1921:56.

**MATERIAL DEPOSITED.**—USNM E17677 (2 spec.).

**DISTRIBUTION.**—Ten specimens collected on the reef flat in the south *Penicillus* zone (station 5), in the coral rubble of the coral-head/coral-pavement zone (station 6), and from just inside the reef crest (station 7). One specimen also collected on the reef crest in the rubble of the coral berm (station 8).

**REMARKS.**—Previously reported from Light-house Reef and Glover's Reef (Devaney, 1974: 141).

### *Ophioderma brevispinum* (Say)

*Ophiura brevispina* Say, 1825:149.—Lyman, 1865:18.—Rathbun, 1879:151.—Ives, 1889:175.—Verrill, 1899a:4.—Brooks and Grave, 1899:83, pls. 1, 2: figs. 1-5.—H. L. Clark, 1901:242.

*Ophiura olivacea* Ayres, 1852:134.

*Ophioderma serpens* Lütken, 1859:86, pls. 1, 2: fig. 6a-c.

*Ophiura olivacea*.—Lütken, 1859:96.—Grave, 1899:92, figs. 1-5.

*Ophioderma olivaceum*.—Ljungman, 1866:304.

*Ophioderma brevispina*.—Ljungman, 1866:303; 1871:615.—Lyman, 1882:9.—Koehler, 1907:281; 1913:354; 1914:1, 4, 147.—Fontaine, 1953:204.—Cherbonnier, 1959:261—262, figs. 5a,b, 6a,b.—Tabb and Manning, 1961:566.—Parslow and Clark, 1963:48.—Tommasi, 1970:66.

*Ophioderma brevispinum*.—H. L. Clark, 1915:300; 1919:57, 72; 1933:40, 70; 1941:89.—Engle, 1939:5, 9.—A. H. Clark, 1954:377.—Ziesenhenne, 1955:188, 198.—Roa, 1967:294, fig. 24.—Godcharles, 1971:28, 33.—Godcharles and Jaap, 1973:57.—Stancyk, 1973:10.

MATERIAL DEPOSITED.—USNM E17649 (1 spec.).

DISTRIBUTION.—One specimen was collected in the north *Penicillus* zone under rubble (station 4).

REMARKS.—The specimen was orange in life but has lost all color in alcohol. This species is known to have a vitellaria larva (Brooks and Grave, 1899).

### *Ophioderma cinereum* Müller and Troschel

*Ophioderma cinereum* Müller and Troschel, 1842:87.—Ljungman, 1866:304; 1871:615.—Koehler, 1913:354.—H. L. Clark, 1915:301; 1918:337; 1919:57, 72; 1933:40, 71; 1942:379.—A. H. Clark, 1922:212; 1939a:452; 1954:377.—Boone, 1933:115-116, pls. 68, 69.—Engel, 1939:5, 9.—Caso, 1951:219, 221, 243, 249, figs. 11-14; 1953:215, 222; 1961:157-162, figs. 61-64.—Ziesenhenne, 1955:187, 192.—da Costa and da Costa, 1962:2.—Thomas, 1962b:65, fig. 1c.—Parslow and Clark, 1963:48.—Roa, 1967:295.—Tommasi, 1970:67.—Godcharles and Jaap, 1973:57.—Devaney, 1974:143.

*Ophioderma antillarum* Lütken, 1859:190, pl. 1: fig. 1a-c..

*Ophiura cinerea*.—Lyman, 1865:27.—Verrill, 1868:367.—Rathbun, 1879:150.—Ives, 1889:175; 1890:331 1891:339.—Stearns, 1891:iv.—Verrill, 1899a:6.—H. L. Clark, 1901:242.

*Ophioderma cinerea*.—Koehler, 1907:281; 1914:1, 6, 9, 147.—A. H. Clark, 1921:57.

*Ophiocryptus hexacanthus* H. L. Clark, 1915:64.

MATERIAL DEPOSITED.—USNM E17856 (9 spec.)

DISTRIBUTION.—Collected among the discarded conch shells at the foot of the pier on the lagoon

side of Carrie Bow Cay (station 1) and just inside the reef crest (station 7).

REMARKS.—Previously reported from Belize (Koehler, 1914:147), Turneffe Islands, Light-house Reef, and Glover's Reef (Devaney, 1974:143).

### *Ophioderma guttatum* Lütken

PLATE 5: top right

*Ophioderma guttata* Lütken, 1859:95, pl. 1: fig. 8a,b.

*Ophiura guttata*.—H. L. Clark, 1901:251.

*Ophiura guttatum*.—H. L. Clark, 1915:301; 1919:57, 72.

*Ophioderma guttatum*.—Ljungman, 1866:303.—H. L. Clark, 1933: 40, 72.—Ziesenhenne, 1955:186, 189.—Thomas, 1962b:65, fig. 1a.—Zeiller, 1974:108 [color fig.].

MATERIAL DEPOSITED.—USNM E17684 (2 spec.); USNM E17685 (1 spec.); USNM E17777 (1 spec.); USNM E17778 (1 spec.).

DISTRIBUTION.—Five specimens collected by Kjell Sandved just inside the reef crest (station 7), and on the reef crest in the rubble of the coral berm (station 8).

### *Ophioderma phoenium* H. L. Clark

PLATE 5: top right

*Ophioderma phoenium* H. L. Clark, 1918:333, pl. 6: figs. 1, 2; 1919:57, 72, pl. 3: fig. 1; 1933:40, 71.—Ziesenhenne, 1955:187, 192.—Devaney, 1974:144.

MATERIAL DEPOSITED.—USNM E17690 (1 spec.); USNM E17776 (1 spec.); USNM E17781 (1 spec.).

DISTRIBUTION.—Three specimens collected on the reef crest in the rubble of the coral berm (station 8).

REMARKS.—Previously reported from Light-house Reef (Devaney, 1974:144).

### *Ophioderma rubicundum* Lütken

FIGURE 178b; PLATE 5: top right

*Ophioderma rubicundum* Lütken, 1856a:8; 1859:192, pl. 1: fig. 2a-c.—Ljungman, 1866:304.—H. L. Clark, 1915:302; 1919:57, 72; 1933:40, 71.—A. H. Clark, 1922:213; 1939a:452; 1954:377.—Ziesenhenne, 1955:187, 197.—Roa, 1967:295.—Devaney, 1974:144.

*Ophiura rubicunda*.—Verrill, 1899a:6.—H. L. Clark, 1901:242.  
*Ophioderma rubicunda*.—Koehler, 1907:282; 1914:1, 7, 148.—  
 A. H. Clark, 1921:57.

MATERIAL DEPOSITED.—USNM E17683 (1 spec.); USNM E17687 (2 spec.).

DISTRIBUTION.—Collected by Kjell Sandved just inside the reef crest (station 7) and on the reef crest in the rubble of the coral berm (station 8). Collected in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10), from the outer ridge of the outer fore reef (station 12), and from the fore-reef slope at 26 to 28 m (station 13).

REMARKS.—Previously reported from Lighthouse Reef and Glover's Reef (Devaney, 1974: 144).

### *Ophioderma squamosissimum* Lütken

*Ophioderma squamosissimum* Lütken, 1856a:8; 1859:92, pl. 1: fig. 7a,b.—Ljungman, 1866:304; 1871:615.—H. L. Clark, 1915:302; 1918:335, pl. 4: fig. 1, pl. 6: figs. 3, 4; 1919:57, 69, 72, pl. 3: fig. 2; 1933:72.—Ziesenhenne, 1955:187, 189.—Thomas, 1962b:62, fig. 1b.—Parslow and Clark, 1963:27.—Godcharles and Jaap, 1973:57.—Zeiller, 1974: 108 [color fig.].

MATERIAL DEPOSITED.—CBC 75.5.15-1 (1 spec.); CBC 75.5.24 (1 spec.) (not catalogued).

DISTRIBUTION.—Found inside the sponge *Pseudoceratina crassa* (Hyatt) collected by K. Rützler on the inner-reef slope near station 11, 20 m (15 May 1975); also found by B. Spracklin on a lagoon patch reef, 1 km WSW of Carrie Bow Cay, 4 m (24 May 1975).

REMARKS.—Specimen CBC 75.5.15-1 has a disc diameter of 7 mm and an arm length of approximately 26 mm measured from the edge of the disc. The upper arm plates form five rows. The radial shields are exposed and consist of well-formed single plates. The sixth arm segment is just outside the margin of the disc and bears five spines on the side arm plates. The oral shields are exposed. There are no supplementary oral shields. The adoral shields carry a few large granules. A translucent gelatinous cuticle coats the entire

exterior including spines, granules and oral papillae. The color in alcohol is white.

Specimen CBC 75.5.24 has a disc diameter of 35 to 38 mm. The arms are approximately 7 mm thick at the edge of the disc. Arm length from the edge of the disc is roughly approximated as 135 mm. There is no noticeable gelatinous cuticle. Supplementary oral shields present distal to the oral shields. Upper arm plates form seven rows. There are six spines on the ninth arm segment just outside the disc. The adoral shields are concealed by the oral shields. There are no single conspicuous plates readily identifiable as radial shields; instead, a large number of small plates bordered by granules occur in the general area of the arm bases and on the aboral interradial peripheral half of the disc. The central area of the aboral disc and the oral interradial areas are completely covered by granules similar to those present in *Ophioderma guttatum*.

### *Ophioderma* species

FIGURE 179

MATERIAL DEPOSITED.—USNM E17788 (1 spec.); USNM E17789 (1 spec.).

DISTRIBUTION.—USNM E17788 collected on the reef flat under rocks in the north *Penicillus* zone (station 4); USNM E17789 on the reef flat under rocks in the south *Penicillus* zone (station 5).

REMARKS.—USNM E17788 has 15.8 mm disc diameter; upper arm plates entire; adoral shields bare; three small radial shields bare; 10 and 11 blunt-tipped arm spines on arm segments eight through 16, lowermost arm spine longest.

Although the specimen keys to *Ophioderma rubicundum* following Ziesenhenne (1955), it compares more favorably with *O. appressum* in total morphology and habitat. The color is mottled greenish brown and, as also found by Devaney (1974) at Lighthouse Reef and Glover's Reef, almost all *O. appressum* at Carrie Bow Cay have adoral shields free of granules. The absence of granules on three radial shields leaves identification problematic.

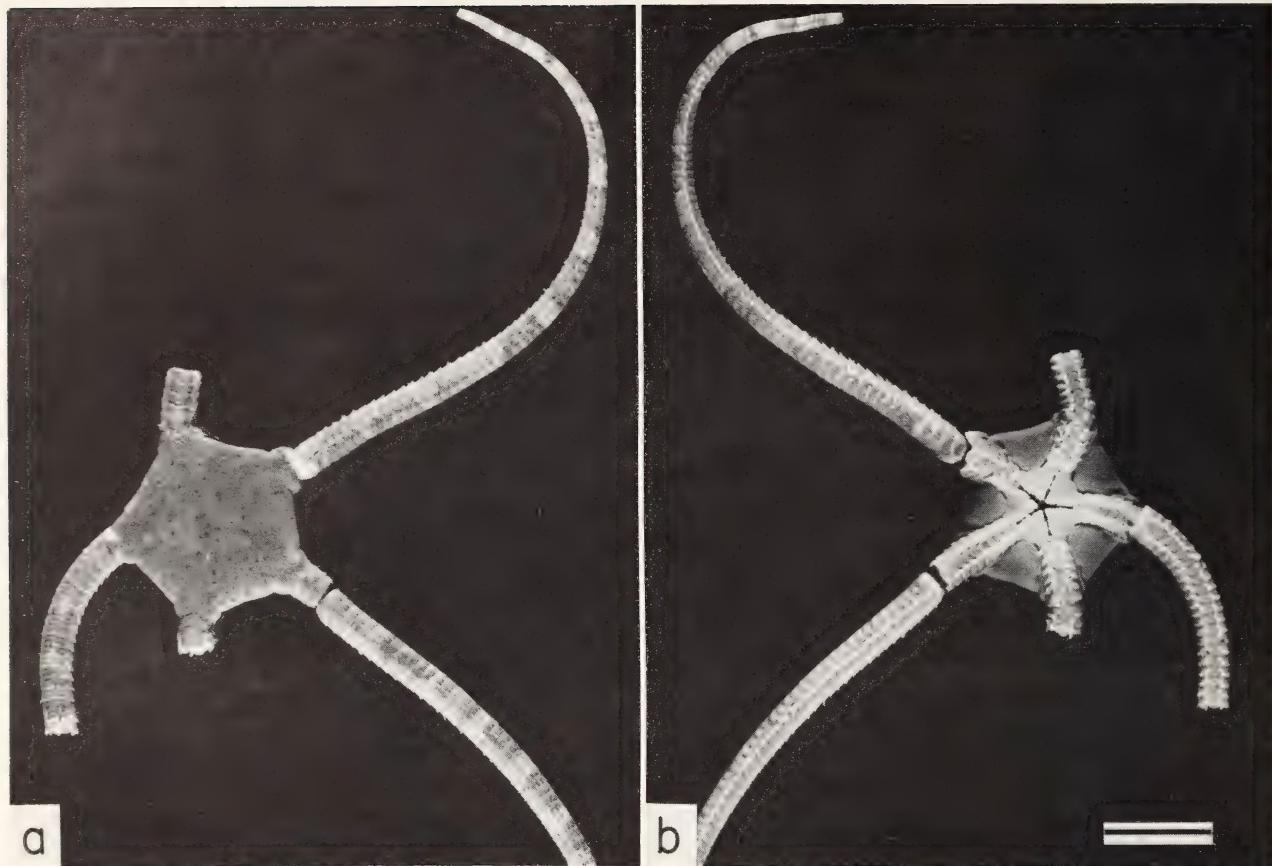


FIGURE 179.—*Ophioderma* sp., USNM E17788, dry. (Scale = 10 mm.)

USNM E17789 agrees in all respects with the above except that all radial shields are covered by granules.

#### *Ophioderma* species, juvenile

FIGURE 180

MATERIAL DEPOSITED.—USNM E17686 (1 spec.).

DISTRIBUTION.—Collected on the reef flat in the rubble of the coral-head/coral-pavement zone (station 6).

REMARKS.—Disc diameter 3.2 mm; upper arm plates entire; radial shields and adoral shields covered by granules; disc granules do not extend onto any part of the arms; arm spines five, less than half an arm segment long, conical, sharply pointed, of equal length; arm tips flattened.

The arm spines resemble those of both *O. brevicaudum* and *O. brevispinum*. The former, however, has relatively shorter arm segments and is said to pass through an *Ophiocryptus* stage with granules on the arms (A. H. Clark, 1939a); the latter has adoral shields free of granules. The upper surface of the disc is red with a central white spot, the lower surface white, and the arms banded red and white. Identification is problematic.

#### *Ophiurochaeta littoralis* (Koehler)

*Ophiolimna littoralis* Koehler, 1913:370, pl. 21: figs. 1-3; 1914: 3, 96, 111.

*Ophiotreta littoralis*.—H. L. Clark, 1915:216; 1919:56; 1933: 34, 43.—A. H. Clark, 1954:377.—Parslow and Clark, 1963:26.

*Ophiurochaeta littoralis*.—Matsumoto, 1917:316-317.—Devaney, 1974:147, figs. 10-12.

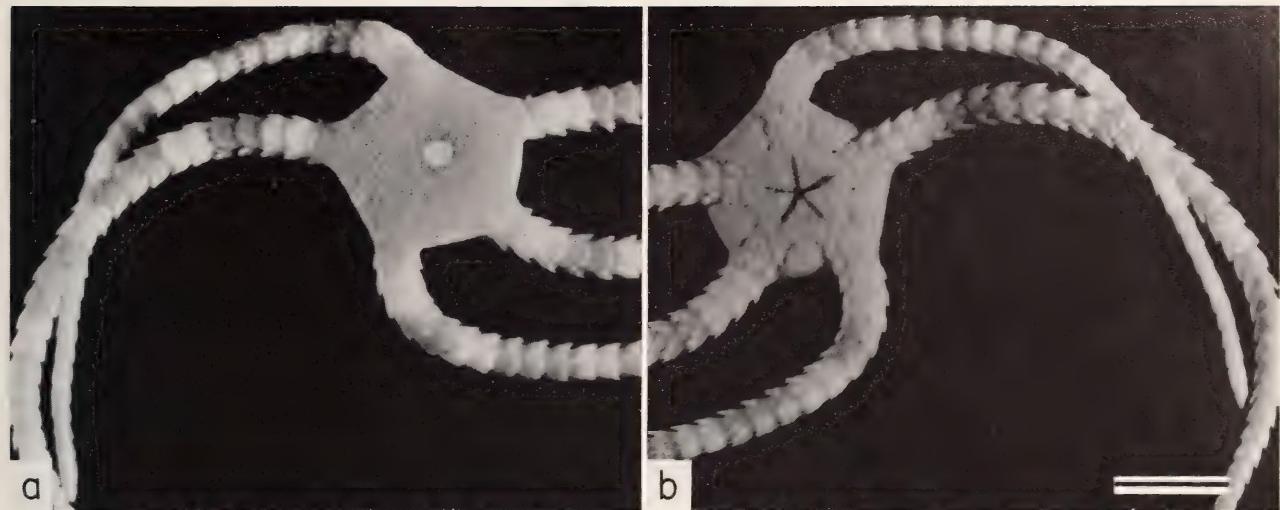


FIGURE 180.—*Ophioderma* sp., juvenile, USNM E17686, dry. (Scale = 2 mm.)

MATERIAL DEPOSITED.—USNM E17795 (1 spec.); USNM E17806 (1 spec.); USNM E17810 (1 spec.).

DISTRIBUTION.—Collected in the spur and groove zone of the inner fore reef from a coral bulk sample taken in 10 to 12 m of water (station 10), and from the fore-reef slope in 26 and 28 meters of water (station 13).

REMARKS.—Presence of young in the bursa of specimen USNM E17795 suggests but does not prove viviparity. Previously reported from Light-house Reef and Glover's Reef (Devaney, 1974: 147).

## Family OPHIURIDAE

### *Ophiolepis impressa* Lütken

*Ophiolepis impressa* Lütken, 1859:203, pl. 2: fig. 3a,b.—Ljungman, 1866:306.—Devaney, 1974:154, figs. 13–15.

*Ophiozona impressa*.—Lyman, 1865:64.—Verrill, 1899a:8.—H. L. Clark, 1901:242; 1915:337; 1919:57, 72; 1933:41, 73.—Koehler, 1907:289; 1914:2, 11, 150.—Matsumoto, 1915:82; 1917:298, 389.—A. H. Clark, 1921:57; 1922:213; 1939a:452; 1954:378.—Engel, 1939:5.—Fell, 1960:33.—Roa, 1967:296.—Tommasi, 1970:74.

MATERIAL DEPOSITED.—USNM E17848 (2 spec.); USNM E17852 (3 spec.).

DISTRIBUTION.—Collected on the back reef in the patch-reef zone of the study transect (station

3); on the reef flat in the north and south *Penicillus* zones (stations 4 and 5), in the coral-head/coral-pavement zone (station 6); just inside the reef crest (station 7), and on the reef crest in the rubble of the coral berm (station 8). One small specimen was extracted from a bulk sample from the outer ridge of the outer fore reef (station 12).

REMARKS.—Previously reported from Light-house Reef and Glover's Reef (Devaney, 1974: 154).

### *Ophiolepis paucispina* (Say)

*Ophiura paucispina* Say, 1825:149.

*Ophiolepis paucispina*.—Müller and Troschel, 1842:90.—Lütken, 1859:204–206, pl. 2: fig. 2a,b.—Lyman, 1865:55.—Ljungman, 1866:306; 1871:618.—Verrill, 1868:367; 1899b:373.—Rathbun, 1879:151.—H. L. Clark, 1901:251; 1915:343; 1919:57, 72; 1933:41, 74; 1942:379.—Koehler, 1907:287; 1913:355; 1914:2, 11, 149.—A. H. Clark, 1921: 32, 44, 50, 58, 62; 1939a:452; 1954:378.—Engel, 1939:5, 9.—Fontaine, 1953:205.—Parslow and Clark 1963:48.—Tommasi, 1970:73, 92.—Devaney, 1974:155.

MATERIAL DEPOSITED.—USNM E17740 (1 spec.); USNM E17760 (8 spec.).

DISTRIBUTION.—Twenty-nine specimens collected among the discarded conch shells at the foot of the pier on the lagoon side of Carrie Bow Cay (station 1).

REMARKS.—The presence of arm tips of mini-

ture young protruding through the genital slits in three deposited specimens probably indicates that this species is viviparous. Collected by Devaney (1974:155) at Lighthouse Reef.

### Conclusions

The following species are reported for the first time from Belize: *Astrophyton muricatum*, *Ophiomittella glabra*, *Sigsbeia murrhina*, *Amphiura fibulata*, *A. stimpsonii*, *Axiognathus squamatus*, *Ophiotigma* sp. (undescribed), *Ophiactis algicola*, *Ophionereis squamulosa*, *Ophiocomella ophiactoides*, *Ophiopsila riisei*, *Ophioderma anitae*, new species, *O. brevispinum*, *O. guttatum*, *O. squamosissimum*. Only *Ophioderma anitae* and *Ophiocoma paucigranulata* can at this time be considered possibly endemic to this part of the Gulf of Honduras. The fauna is otherwise widely distributed throughout the Greater and Lesser Antilles (Parslow and Clark, 1963), as might be expected from the general westerly flow of water

through the Caribbean (Duncan et al., 1977; Metcalf et al., 1977).

Although many species are found in all the major physiographic parts of the reef, nevertheless the rank-order distributions show certain qualitative and quantitative trends from lagoon to fore reef. Table 29 is an attempt to characterize the composition and facies of the ophiuroid fauna present in four main physiographic areas of the reef. The distribution of individual species over the study area has been given in the preceding systematic section. Because no quantitative sampling was undertaken, the actual numbers of specimens of any species collected are not meaningful. Very common species were not collected on every encounter, and the discovery of a previously unrepresented species usually initiated an attempt to secure additional specimens. It appears, however, that this distortion of actual and relative abundances has not greatly upset the rank order of abundances. My subjective impres-

TABLE 29.—Rank-order abundances of ophiuroids within major physiographic areas near Carrie Bow Cay (station numbers in parentheses, species arranged in each column in decreasing order of abundance, vertical bars connect species represented equally)

Lagoon (1, 2)	Reef flat, back reef (3-7)	Reef crest (8, 9)	Fore reef (10-13)
<i>Ophiothrix oerstedi</i>	<i>Ophioderma appressum</i>	<i>Ophiocoma wendti</i>	<i>Ophiocoma pumila</i>
<i>Ophiactis savignyi</i>	<i>Ophiocoma echinata</i>	<i>Ophiocoma paucigranulata</i>	<i>Ophiothrix angulata</i>
<i>Ophiothrix angulata</i>	<i>Ophiolepis impressa</i>	<i>Ophiocoma pumila</i>	<i>Ophioderma rubicundum</i>
<i>Ophiolepis paucispina</i>	<i>Ophiocoma wendti</i>	<i>Ophiocoma echinata</i>	<i>Ophiurochaeta littoralis</i>
<i>Ophiocoma pumila</i>	<i>Ophiocoma pumila</i>	<i>Ophioderma appressum</i>	<i>Ophiopsila riisei</i>
<i>Ophiocomella ophiactoides</i>	<i>Ophioderma rubicundum</i>	<i>Ophioderma anitae</i>	<i>Ophiactis savignyi</i>
<i>Axiognathus squamatus</i>	<i>Ophiomyxa flaccida</i>	<i>Ophiothrix oerstedi</i>	<i>Ophiothrix suensonii</i>
<i>Amphiura stimpsonii</i>	<i>Ophioderma brevicaudum</i>	<i>Ophiolepis impressa</i>	<i>Ophiothrix oerstedi</i>
<i>Ophionereis reticulata</i>	<i>Ophiothrix oerstedi</i>	<i>Ophioderma phoenium</i>	<i>Sigsbeia murrhina</i>
<i>Ophioderma cinereum</i>	<i>Ophionereis squamulosa</i>	<i>Ophioderma guttatum</i>	<i>Amphiura stimpsonii</i>
<i>Ophiocoma echinata</i>	<i>Ophiocomella ophiactoides</i>	<i>Ophiomyxa flaccida</i>	<i>Ophiocoma echinata</i>
<i>Ophiotigma</i> sp.	<i>Ophionereis reticulata</i>	<i>Ophioderma rubicundum</i>	<i>Ophiocoma wendti</i>
<i>Ophiocoma wendti</i>	<i>Ophioderma cinereum</i>	<i>Ophiomitrella glabra</i>	<i>Ophionereis reticulata</i>
<i>Amphiura fibulata</i>	<i>Ophioderma guttatum</i>	<i>Ophioderma brevicaudum</i>	<i>Ophiotigma</i> sp.
<i>Ophioderma appressum</i>	<i>Ophiactis savignyi</i>		<i>Astrophyton muricatum</i>
<i>Ophionereis squamulosa</i>	<i>Ophioderma</i> sp.		<i>Ophiomyxa flaccida</i>
	<i>Ophiothrix angulata</i>		<i>Ophiomitrella glabra</i>
	<i>Ophioderma brevispinum</i>		<i>Ophiocoma paucigranulata</i>
	<i>Ophioderma</i> sp., juv.		<i>Ophiolepis impressa</i>
			<i>Ophiactis algicola</i>
			<i>Ophionereis squamulosa</i>
			<i>Ophioderma squamosissimum</i>

sion is that the most common species in the field are the most common in the collection (and conversely for the least common), but Table 29 should only be considered an approximation for a number of reasons. Subjective field impressions involve psychometric aspects such as size and visibility which may only partly correlate with actual numbers of individuals. Certain species may be very adept at escaping collection with the hand methods employed. Although these results should be used with caution, they seem worth presenting, because I have not found any other attempts at rank ordering the species of ophiuroids by general habitat for the West Indian region. Species are listed in the table in decreasing level of abundance, with a vertical bar connecting those equally represented by numbers of specimens in the collection.

The ophiuroids found among discarded conch shells on the lagoon side of the island (station 1) are mainly small or minute species. It is notable that of the minute species three are fissiparous (*Ophioactis savignyi*, *Ophiocomella ophiactoides*, and *Ophiostigma* sp.) and two (probably three) are viviparous (*Axiognathus squamatus*, *Amphiura stimpsonii*, and *Ophiolepis paucispina*). The species of ophiuroids found on the reef flat (stations 4–6), including those from the inner reef crest zone (station 7), and the patch reef zone (station 3) are dominated by the families Ophiodermatidae, Ophiocomidae and Ophiuridae and the principal habitat is beneath coral, coral rock, or dead shells. The species of ophiuroids found on the reef crest, principally in the rubble of the coral berm (station 8), but also just seaward (station 9), are dominated by the families Ophiocomidae and Ophiodermatidae. It is likely that *Ophiocoma paucigranulata* is significantly overrepresented in the reef crest collection because once discovered, it was deliberately sought. The species of ophiuroids found on the fore reef—the spur and groove zone (station 10), the trough (station 11), the outer ridge (station 12), and also the accessible part of the fore reef slope (station 13)—are notable for the strong representation of epizootic species not found shallower, especially *Astrophyton muricatum*,

*Sigsbeia murrhina*, *Ophiothrix suensonii*, *Ophiopsila rieseii*, and *Ophiurochaeta littoralis*. Still, there is sufficient crevice habitat to support the presence of species of *Ophiocoma*, *Ophionereis*, and *Ophiolepis*, which are found principally under coral rock in shallower water.

Although the reproductive biology of the ophiuroids of Carrie Bow Cay needs further extensive investigation, the discovery of young in the bursae of *Ophiurochaeta littoralis* and *Ophiolepis paucispina* and the confirmation of fissiparity in West Indian *Ophiostigma* deserve comment at this time. The presence of young in genital bursae suggests but does not prove that these ophiuroids are viviparous. The counter example was provided by Smith (1938) in the case of *Ophiothrix fragilis*, which has a planktotrophic ophiopluteus larva. Smith found very young post larvae clinging to the oral interbrachial arm spines and slightly older post larvae present in the bursae of a small percentage of the adult population. Similarly, A. H. Clark (1939a) found young post larvae comparably located on the spines of *Ophiothrix hartfordi* from Puerto Rico. The young post larvae of *Ophiurochaeta littoralis* and *Ophiolepis paucispina* may somehow preferentially settle from the plankton onto the adults, but the mechanism for such action is difficult to identify. The subsequent presence of young post larvae in bursae may be interpreted (in accord with Smith) as the result of crevice-seeking behavior.

This possible strategy seems less applicable to *Ophiolepis paucispina* than to *Ophiurochaeta littoralis* because a relatively large proportion of the ophiuroids comparable in size with *O. paucispina* in the habitat of discarded conch shells practice direct recruitment through either viviparity or fissiparity, as noted above. This aspect of the minute ophiuroids of this habitat is highlighted not only by the possibility that *O. paucispina* is viviparous, but also by the presence of exclusively fissiparous specimens of *Ophiostigma* sp. A. M. Clark (1967a) did not include *Ophiostigma* in her list of fissiparous ophiuroids, presumably because she tentatively referred the fissiparous specimen of *Ophiostigma* recorded by H. L. Clark (1942) from

Bermuda to *Ophiocomella ophiactoides* (see Parslow and Clark, 1963). In my opinion, however, the generic identity of the present fissiparous speci-

mens is certain, although they seem to represent an undescribed species rather than *Ophiotigma isacanthum*.

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# Shallow-Water Crinoidea (Echinodermata) from Carrie Bow Cay, Belize

D. Bradford Macurda, Jr.

## ABSTRACT

Four species of shallow-water crinoids occur on the barrier reef off Carrie Bow Cay, Belize: *Nemaster discoidea*, *N. rubiginosa*, *Ctenantedon kinziei*, and *Analcidometra armata*. The distribution of these animals within the reef environment is determined by water movement and depth. The number of color variants of the two species of *Nemaster* is as high as found at most localities in the West Indies. The discovery of *Ctenantedon kinziei* extends considerably the range of this species.

## Introduction

Although several species of crinoids have long been known from the Caribbean area (see, for example, Clark, 1921), the shallow-water crinoids of the West Indies were a virtually unknown part of the reef fauna until D. L. Meyer began to study them in the late 1960s. Work by Meyer and myself in the 1970s revealed the ubiquity of these animals from the Bahamas to the South American coast and from Central America to Barbados. Detailed studies have been published for the Bahamas (Macurda, 1973; 1975), Jamaica (Meyer, 1973a), and Colombia (Meyer and Macurda, 1976). More general accounts for the Caribbean are found in Meyer (1973b), for the West Indies in Macurda and Meyer (1977). The overall distribution of shallow- and deep-water crinoids of

the West Indies was recently reviewed on the basis of extensive new collections made during the 1960s and 1970s (Meyer et al., 1978).

Eight species of shallow-water crinoids belonging to five genera are found in the Caribbean. *Nemaster* is represented by three species: *N. discoidea* (Carpenter), *N. grandis* Clark, and *N. rubiginosa* (Pourtales); *Comactinia* by two: *C. echinoptera* (Müller) and *C. meridionalis meridionalis* (Agassiz); and the following genera by single species: *Analcidometra armata* (Pourtales), *Ctenantedon kinziei* Meyer, and *Tropiometra carinata* (Lamarck). David L. Meyer (pers. comm.) identified *Neocomatella* sp. from one shallow-water station in Panama but no one has found a representative of this genus again above 50 m. *Tropiometra carinata*, in the Caribbean, is found only in the southern and eastern parts, but it occurs elsewhere in the southwestern Atlantic. Shallow-water *Comactinia meridionalis meridionalis* is known only from Panama and the Carolinas. *Nemaster grandis* occurs in the western and central Caribbean. The remaining five species are found in reef environments throughout the West Indies. All eight species are illustrated in Macurda and Meyer (1977).

**ACKNOWLEDGMENTS.**—I wish to thank B. W. Spracklin and K. M. Muzik for collecting, and C. G. Messing for identifying two specimens of *Analcidometra armata* that were found off Carrie Bow Cay subsequent to my visit. I am also indebted to D. L. Meyer for extensive discussions of crinoid taxonomy and ecology. This research was conducted under National Science Foundation Grant GB-36439.

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## Carrie Bow Cay Crinoids

Dredging does not permit accurate determination of the taxonomic composition and relative abundance of crinoids in reef environments because of the cryptic habits of many species. Divers using SCUBA must make transects for direct observation and counts, and break apart coral rock to find cryptic species, such as *Ctenantedon kinziei* and *Comactinia echinoptera*. Most of the following data for the Carrie Bow Cay area were obtained from 11 dives on the fore reef east of South Water Cay, Carrie Bow Cay, and Curlew Bank (see Rützler and Macintyre, herein, Figure 2), between 24 and 29 April 1973. Four species of crinoids are present on this section of the Belizean barrier reef: *Nemaster discoidea*, *N. rubiginosa*, *Ctenantedon kinziei*, and *Analcidometra armata*. The first two are far more abundant than the latter two. *Analcidometra*, a small crinoid that lives on gorgonians (primarily *Pseudopterogorgia* spp.), was not seen during my visit but was later collected twice on the fore reef east of Carrie Bow Cay. Another nearby record of this species is from Isla Roatan, Bay Island, Honduras, reported by Macurda and Meyer (1977). These authors also found *Comactinia echinoptera* and *Nemaster grandis* in the Bay Islands; neither species has yet been obtained in Belize.

TABLE 30.—Depth distribution of color varieties of *Nemaster discoidea* and *N. rubiginosa* on outer ridge and fore-reef slope off Curlew Bank and South Water Cay (counts are based on one transect at each location, approximately 2 m wide and conducted over a 45 min dive period; first number of each pair of values is for Curlew Bank)

Color variety	Depth range (m)						Totals
	10–15	15–20	20–25	25–30	30–35	35–40	
<i>Nemaster discoidea</i>							
Dark green				0;9	1;1		1;10
Gold			3;1	3;2	1;3	0;7	7;13
Yellow with black stripe	2;0	5;0		1;3			8;3
<i>N. rubiginosa</i>							
Orange with black stripe	19;23	6;1		0;1	1;0		26;25
Orange with yellow-tipped pinnules	10;4						10;4
Orange with white-tipped pinnules	2;2	1;0					3;2

The profiles surveyed for crinoids run perpendicular to the barrier reef. There is an inner fore reef gradually deepening from the reef crest to 13 m; the bottom then slopes into a sand trough (23 m), rises again to an outer ridge (13 m), and then drops at an angle of 40°–50° along the fore-reef slope to 50 m before becoming vertical (Rützler and Macintyre, herein: 9, Figure 5). The distance from the reef crest to the sand trough is 300 m, the remainder of the profile covers an additional 100 m.

Both *Nemaster* species are abundant on the fore-reef slope and on the top of the outer ridge but not on its shoreward face, the sand trough, or the deeper part of the inner reef slope. They become abundant again in the spur and groove zone of the inner fore reef between 10 and 15 m, but are not found shallower than this. The depth distribution of these species reflects their need of moderate water motion without direct wave surge. Commensals include ophiuroids, myzostomes, and shrimps.

*Nemaster discoidea* and *N. rubiginosa* are rheophobic crinoids that hide the calyx beneath a coral or within a crevice and then extend some of the arms into the surrounding water in order to catch microscopic particles. A variety of substrates is used to hide the disc. Pinnules are regularly arrayed in a tetrad; the arms do not form a regular

TABLE 31.—Arm length and arm number of color varieties of *Nemaster discoidea* and *N. rubiginosa* from Carrie Bow Cay

Color variety	Average arm length (mm)	Average arm number	Sample size
<i>Nemaster discoidea</i>			
Dark green	127	17	4
Gold	117	18	11
Yellow with black stripe	130	19	9
<i>N. rubiginosa</i>			
Orange with black stripe	141	21	41
Orange with yellow-tipped pinnules	84	21	24
Orange with white-tipped pinnules	70	21	10

fan as in rheophilic crinoids (see Macurda and Meyer, 1977, figs. 1, 2). Arm lengths are commonly asymmetric owing to restricted space for some of the arms to grow. *Nemaster rubiginosa*, predominant in shallow water, is gradually replaced by *N. discoidea* with depth. Several persistent, easily recognizable color varieties of each are known and also present off Carrie Bow Cay (Tables 30, 31). There are three distinct color varieties of *N. discoidea*: a form with dark green arms, a form with gold arms, and a form with yellow arms with an intermittent black stripe. All have black-tipped pinnules. The dark green variety is found on the fore-reef slope between 18 and 40 m (maximum observed range is larger than transect data given in Table 30). The gold form ranges from 13 m on top of the outer ridge (very rare) to 40 m depth on the fore-reef slope; it is the most abundant variety. The unusual yellow form with black stripes occurs on the fore-reef slope between 13 and 28 m. The arms of this species are always extended into the surrounding water.

*Nemaster rubiginosa*, the most abundant crinoid, occurs primarily on the outer ridge and in the spur and groove zone (Plate 4: bottom right). It appears in at least seven color varieties, of which only three are common (Table 30): orange with black stripe, orange with yellow-tipped pinnules,

and orange with white-tipped pinnules. The black-striped form is the most common one and is particularly abundant on the outer ridge. It is the only variety to extend its range down the fore-reef slope, to 33 m, although it is rare below 16 m. The forms with yellow and white pinnule tips are more common at the spur and groove zone than on the outer ridge. The yellow-tipped variety is the more abundant but also the more cryptic of the two. The arms of *N. rubiginosa* are stouter than those of *N. discoidea* and may reach 300 mm in length, although 200 mm was the longest observed off Belize. There, this species is mostly confined to heads of the coral *Montastrea annularis* (Ellis and Solander), unlike Panama where it occurs among *Acropora cervicornis* (Lamarck).

*Ctenantedon kinziei* is rare (five individuals observed) but its discovery in Belize is important because this species was unknown until Meyer (1972) described it from the southern Caribbean. We have since discovered it throughout the West Indies. In Belize, it occurs from on top of the outer ridge and down the fore-reef slope, from 13 to 25 m, completely hidden within coral heads such as are formed by the species of *Montastrea*.

Two specimens of *Analcidometra armata* were discovered on gorgonians after my survey of 1973. One was found on *Muriceopsis* sp. on the fore-reef slope in 20 m (B. W. Spracklin, May 1975), the second on *Gorgonia mariae* Bayer in the low-relief spur and groove zone in 11 m (K. M. Muzik, April 1979).

### Conclusion

My investigations revealed that only four of the five most common Caribbean shallow-water crinoids are present at Carrie Bow Cay. Similar work should be conducted at other localities to ascertain the possible presence of additional species before the results of this study can be accepted as a definitive reflection of crinoid diversity on the Barrier reef of Belize.

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# Chemical Defense in Tropical Marine Algae

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## ABSTRACT

Chemical and taxonomic studies of the benthic algae of Carrie Bow Cay, Belize, have revealed that species of certain families of the Rhodophyta, Phaeophyta, and Chlorophyta produce unique or unusual secondary compounds. Analysis of the structural organic chemistries of these natural products shows that the substances produced consist largely of halogenated and non-halogenated terpenoids including monoterpenoids ( $C_{10}$  compounds), sesquiterpenoids ( $C_{15}$  compounds), and diterpenoids ( $C_{20}$  compounds), and larger compounds of mixed acetate-mevalonate origin. These secondary compounds, hypothesized to be feeding deterrents developed as defenses against herbivores, were examined for antibiotic activity and toxicity. Fish toxicity experiments using *Eupomacentrus leucostictus* and these compounds revealed sublethal to lethal effects. One compound, elatol, from *Laurencia obtusa* was found to inhibit sea urchin egg development totally. Field observations indicate that marine algae having these secondary metabolites are not eaten by many herbivores, and biological activity testing suggests that certain of these compounds may be responsible. In some cases, specialized grazers have apparently co-evolved to tolerate these potential chemical "deterrents," and may in turn use them in their own defense against predation.

## Introduction

Land plants have evolved elaborate morphological and chemical defense mechanisms against

herbivores (Fraenkel, 1959; Whittaker and Feeney, 1971). Since Janzen (1973) put forth the working hypothesis that the primary role of secondary compounds in higher plant vegetation and seeds is defense against herbivores and micro-organisms, it has been generally recognized that these natural products may either serve as feeding deterrents or attractants in terrestrial plant-animal interactions (see, for example, Harbourne, 1977), or function as allelopathic chemicals (Müller, 1970) or antibiotics. The same evolutionary pressures responsible for the many biologically active compounds found in terrestrial vegetation have been predicted to have parallels in marine vegetation (Whittaker and Feeney, 1971; Kittredge, 1976). Predaceous fishes and invertebrate animals have been important forces acting as agents of natural selection in the evolution of protective mechanisms (Bakus, 1964; 1966; 1969).

The world-wide distribution of herbivorous marine fishes shows a concentration, both in species diversity and biomass, on tropical reefs (Hiatt and Strasburg, 1960). Herbivorous fishes generally dominate fish communities on tropical reefs (Bardach, 1959; Hiatt and Strasburg, 1960); and the number and biomass of both vertebrate and invertebrate herbivores are two of the striking features of Caribbean coral reefs (Ogden, 1976).

Marine algae have developed several defenses in response to herbivory (see for example, Paine and Vadas, 1969; Vadas, 1977; 1979). Algal species may deter herbivores in one or more of the following ways: (1) by having a resistant or unpalatable physical structure (for example, the calcareous nature of some Rhodophyta, Chloro-

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phyta, and Phaeophyta, or the tough texture of certain Phaeophyta), or a morphology that makes it difficult for the herbivore to attach to feed (see Hay, 1981); (2) by residing in habitats that are cryptic or unfavorable for herbivore feeding (Ogden et al., 1973; Adey and Vassar, 1975), such as in crevices where they are inaccessible, in areas of high surf or strong surge where herbivores cannot attach themselves for feeding, or in areas where herbivores are subject to increased predation; (3) by having heteromorphic life histories, with a fast growing stage and a resistant stage (Lubchenco and Cubit, 1980); (4) by living in association with toxic or unpalatable algae (see plant defense guilds of Atsatt and O'Dowd, 1976); (5) by being unpredictable in occurrence in time or space (for example, ephemeral species, or species having rare or patchy distribution) (Littler and Littler, 1980); and/or (6) by producing secondary metabolites (Fenical, 1975), ranging from unpalatable to toxic, as chemical defense against herbivores.

Since the pioneering work of Pratt et al. (1951) reporting antibacterial activity of various seaweed extracts, several investigators have demonstrated the antibiotic activity of extracts from some tropical algae (for example, Burkholder et al., 1960; Olesen et al., 1964; Sieburth, 1964; Burkholder, 1973; Bhakuni and Silva, 1974; Núñez and Serpa Sanabria, 1975). Studies of Boyd et al. (1966) on the effects of selected tropical algae on human erythrocytes found that the extracts from six brown algae agglutinated blood groups O and A. More recently, Targett and Mitsui (1979) studied the effects of aqueous extracts from tropical algae on fish erythrocyte hemolysis and fish mortality, and Targett (1979) developed a behavioral bioassay (gastropod tentacle withdrawal) to test extracts from marine algae for biological activity. In another study, both seasonal variability and locality differences of the tropical algal extract's antibiotic activity against selected pathogenic bacteria was observed (Almodóvar, 1964). Hornsey and Hide (1974) found similar seasonal variation in their screening experiments for antimicrobial activity of British marine algae. Sieburth (1968) offered some ecological interpretation of the role of algal antibiot-

ics in marine algal-algal and algal-animal interactions. Unfortunately, there have been few quantitative studies on the diets of marine herbivores, and our knowledge of feeding behavior and food preferences of tropical herbivores is still too inadequate to be conclusive. What is known on tropical fish diets can be found in Randall (1967), while sea urchin diets have been summarized by Lawrence (1975).

In this paper we provide an overview of interactions between tropical reef algae and herbivores in the Caribbean, with reference to our identification of specific compounds from Belize reef algae. On the basis of the antimicrobial activity and fish toxicity of these compounds we present hypotheses of their ecological role in reef algal-animal interactions.

Over the past four years at Carrie Bow Cay, off the coast of Belize, we have investigated the systematics of the benthic algae as well as the chemical nature of their secondary compounds. Some of the Chlorophyta, Phaeophyta, and Rhodophyta synthesized unusual secondary products which in the laboratory showed biological activity against selected micro-organisms and a reef fish. Many of the relatively abundant algae that were accessible to potential herbivores were found to contain these biologically active substances. We hypothesize that these compounds have been selected for by the intense grazing pressure on tropical marine algae and that they function to minimize population losses by inhibiting or repelling herbivores. Our present analysis indicates that tropical reef algae are chemically defended from many generalist herbivores, while some specialist herbivores have evolved a physiological tolerance to these natural products.

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## Materials and Methods

Field trips were made to Carrie Bow Cay on the barrier reef of Belize ( $16^{\circ}48'N$ ;  $88^{\circ}05'W$ ), during the spring (March–May) of 1976, 1977, and 1978 (for a review of the biological and geological features of Carrie Bow Cay, see Rützler and Macintyre, herein: 9). During each expedition, benthic macro-algae were collected for subsequent studies on their systematics and chemistry. Homogeneous collections were identified and separated into specimens for chemical analysis and vouchers for taxonomic verification; the former were preserved in isopropanol, the latter in 4% Formalin-seawater.

Voucher specimens have been deposited in the U.S. National Herbarium, Smithsonian Institution. The following algal species were chemically investigated in this study. Chlorophyta: *Caulerpa cupressoides* (Vahl) C. Agardh, *C. mexicana* (Sonder) Kützing, *C. racemosa* (Forsskål) J. Agardh, *C. serrulata* (Forsskål) J. Agardh emend Børgesen, *C. sertularioides* (Gmelin) Howe, *C. verticillata* J. Agardh, *Rhipocephalus phoenix* (Ellis and Solander) Kützing, and *Udotea flabellum* (Ellis and Solander) Howe. Phaeophyta: *Dictyota bartayresii* Lamouroux, *Stylopyodium zonale* (Lamouroux) Papenfuss, *Sargassum polyceratim* var. *ovatum* (Collins) Taylor, and *Turbinaria turbinata* (Linnaeus) Kuntze. Rhodophyta: *Liagora farinosa* Lamouroux, *Asparagopsis taxiformis* (Delile) Trevisan; *Ochtodes secundiramea* (Montagne) Howe, *Laurencia caraibica* Silva, and *L. obtusa* (Hudson) Lamouroux.

The biological activity of the secondary compounds produced by the marine algae was investigated by nutrient agar plate disc assay methods in the laboratory of W. Fenical, and by fish toxicity experiments. Antibacterial activity was examined on the basis of inhibition of *Staphylococcus aureus* Rosenbach, *Bacillus subtilis* (Ehrenberg) Cohn, and *Escherichia coli* (Migula) Castellani and Chalmers, and antifungal activity was assessed against the human pathogen *Candida albicans* (Robin) Berkhout. Toxicity to fish was tested using *Eupomacentrus leucostictus* (Müller and Troschel) with serial dilutions of the alga's natural compounds in seawater (as outlined by Sun and

Fenical, 1979), and the crude extract. In each treatment (three replicates), either the extract or the pure compound was added directly to the seawater with the aid of an ethanol dispersant; controls were untreated seawater and seawater containing only the ethanol. Fish mortality within one hour was considered to indicate a toxic compound, and sublethal effects, such as loss of equilibrium and respiratory stress were noted as "strong" or "mild." Results of the anti-microbial and ichthyotoxic experiments are summarized in Table 32.

## Results and Discussion

**CHLOROPHYTA.**—Of the benthic algae in the vicinity of Carrie Bow Cay (Norris and Bucher, herein: 167), the green algae are perhaps the most abundant in biomass, having representatives throughout the diverse intertidal and subtidal habitats. Three families predominate, the Codaceae with species of *Avrainvillea* and *Codium*, Udoteaceae with *Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea*, and the Caulerpaceae with species of its monotypic genus, *Caulerpa*.

The species we investigated from these families produced unusual secondary metabolites. Of six species of *Caulerpa* from Carrie Bow Cay, *C. cupressoides*, *C. mexicana*, *C. racemosa*, *C. serrulata*, *C. sertularioides*, and *C. verticillata*, all but *C. mexicana* contained the known compound caulerpin (Figure 181a, compound I). This substance was originally isolated from *C. racemosa*, *C. serrulata*, and *C. sertularioides* by Aguilar-Santos and Doty (1968). In recent studies of *C. taxifolia* (Vahl) C. Agardh, Maiti and Thomson (1977) re-examined the structure of caulerpin (Aguilar-Santos, 1970) and found it to be a derivatized indole dimer.

We found that species of *Caulerpa*, *Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea* also produce terpenoids of rather complex structure. Although it is difficult to analyze many of these compounds thoroughly because of their instability, we have isolated from *Rhipocephalus phoenix* two sesquiterpenoids, rhipocephenal and rhipocephalin, designated as compounds II and III respectively (Figure 181b). These compounds typify the struc-

TABLE 32.—Compounds identified from tropical benthic algae of Carrie Bow Cay, and results of biological activity tests (compound designations identified in Figures 181, 182; 0 = no response, + = positive response, NT = not tested)

Species	Compound	Antimicrobial activity	Toxicity to fish
<b>CHLOROPHYTA</b>			
<i>Caulerpa cupressoides</i>	I	0	NT
<i>C. racemosa</i>	I	0	+ <sup>1</sup>
<i>C. serrulata</i>	I	0	NT
<i>C. sertularioides</i>	I	0	NT
<i>C. verticillata</i>	I	0	NT
<i>Rhipocephalus phoenix</i>	II	+	+ <sup>2</sup>
<i>R. phoenix</i>	III	+	+
<b>PHAEOPHYTA</b>			
<i>Sargassum polyceratum var. ovatum</i>	IV	+ <sup>3</sup>	NT
<i>Turbinaria turbinata</i>	IV	+	NT
<i>Dictyota bartayresii</i>	V	+	0
<i>Styropodium zonale</i>	VI	+	+
<b>RHODOPHYTA</b>			
<i>Asparagopsis taxiformis</i>	VII	+	NT
<i>Ochthodes secundiramea</i>	VIII	+	NT
<i>O. secundiramea</i>	IX	+	NT
<i>Liagora farinosa</i>	X	+	+
<i>Laurencia caraibica</i>	XI	+ <sup>4</sup>	NT
<i>L. obtusa</i>	XII	+	NT

<sup>1</sup> Lewin, 1970   <sup>2</sup> Sun and Fenical, 1979   <sup>3</sup> Glombitza, 1977   <sup>4</sup> Izac, 1979

tural types we have detected in the Caulerpaceae and in some species of the Codiaceae and Udoteaceae. Compounds II and III were ichthyotoxic at the 2 and 10 µg/ml levels, respectively, against *Eupomacentrus leucostictus*; when these compounds were placed in food offered to this fish it was not eaten (Sun and Fenical, 1979). We are continuing studies with *Halimeda* species, *Udotea flabellum*, *U. conglutinata* (Ellis and Solander) Lamouroux, *Penicillus capitatus* Lamark, and *Avrainvillea longicaulis* (Kützing) Murray and Boodle, each of which appears to contain unique and biologically active secondary metabolites.

Our field observations indicate that the tropical algae of these three families are avoided by most herbivores, at least by the "generalists" (sensu Emlen, 1973). Few quantitative studies have been done on food preferences of tropical fish and invertebrates. Those dealing with the herbivores and green algae we studied (see Lawrence, 1975; Ogden and Lobel, 1978) noted that

the urchin *Echinometra lucunter* (Linnaeus) near St. Croix, Virgin Islands, does not eat *Caulerpa* and *Halimeda*, even though they are available in small amounts on substrate (Juliana and Ambrosetti, 1974; Ogden, 1976) and as drift (D. Abbott et al., 1974). Rates of feeding by *Lytechinus variegatus* (Lamarck) varied in laboratory experiments, with *Caulerpa* being eaten least rapidly when offered alone and most rapidly when offered with five other marine plants; *Halimeda* was consistently the least preferred alga (Lawrence, 1975). Lowe and Lawrence (1976) suggest that *L. variegatus* in Florida may be feeding preferentially on detrital seagrasses. Similarly, Vadas et al. (in press) showed the preferred diet of field populations of *L. variegatus* was detrital *Thalassia*, while siphonaceous greens were largely not eaten (except by one population in which approximately 30% of their diet consisted of these algae). Lowe and Lawrence (1976) suggested a mixed diet might be superior in nutrients for *L. variegatus*.

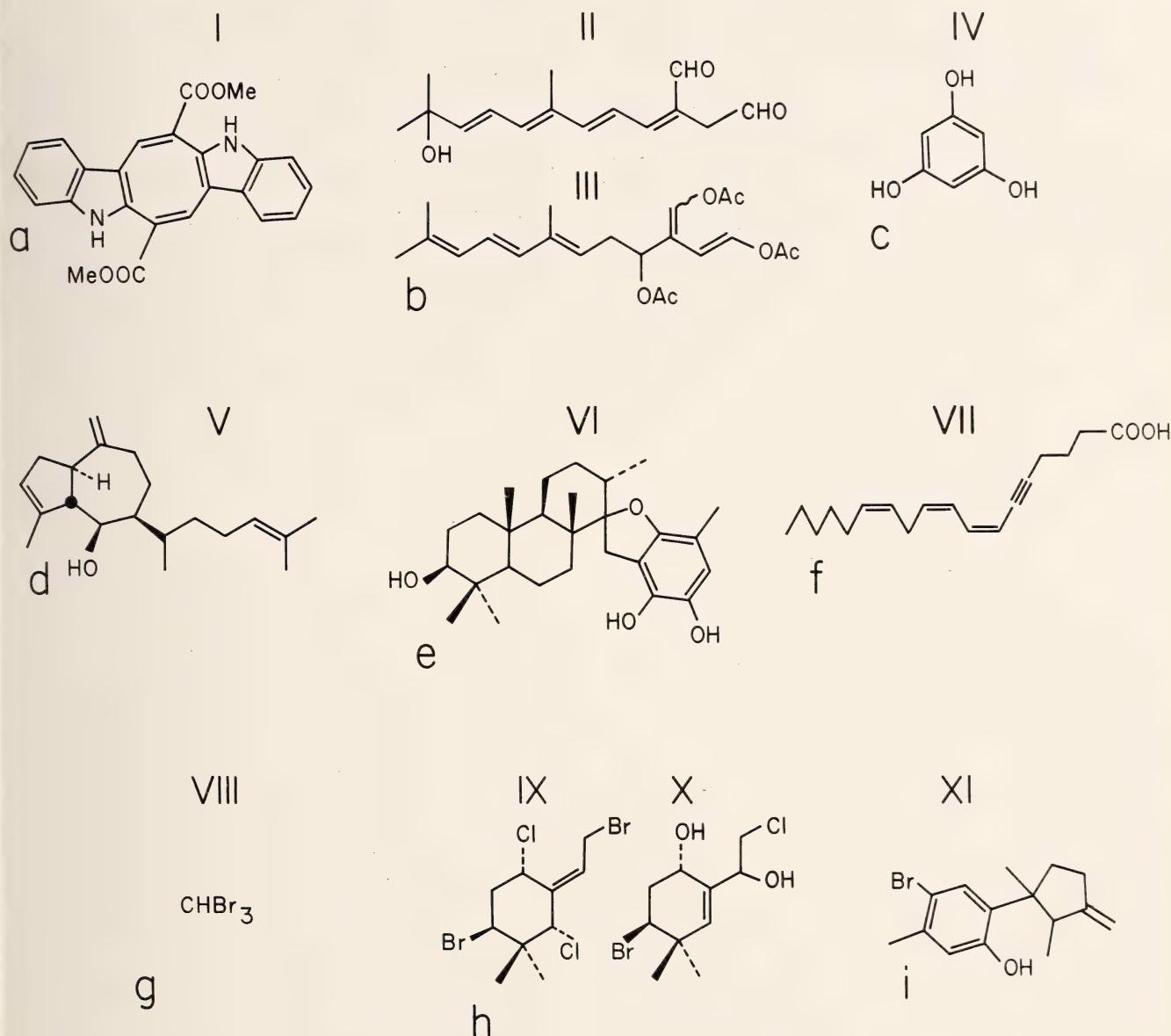


FIGURE 181.—Structures of biologically active metabolites isolated from Carrie Bow Cay marine algae: *a*, caulerpin (compound I) from species of *Caulerpa*; *b*, sesquiterpenoids, rhipocephenal (II) and rhipocephalin (III), from *Rhipocephalus phoenix*; *c*, polyphenol (IV) from *Sargassum* and *Turbinaria*; *d*, pachydictyol A (V) from *Dictyota bartayresii*; *e*, stypotriol (VI) from *Sympodium zonale*; *f*, acetylene containing lipid (VII) from *Liagora farinosa*; *g*, bromoform (VIII) from *Asparagopsis taxiformis*; *h*, polhyalogenated monoterpenoids, ochtodene (IX) and ochtidial (X), from *Ochthodes secundiramea*; *i*, allolaurinterol (XI) from *Laurencia caraibica*.

Lewis (1958) suggested that *Tripterus ventricosus* (Lamarck) refused *Halimeda* because of its calcified structure, but we suggest this rejection may also be due to the chemical component of

*Halimeda*. Green algae not eaten by the urchin *Diadema antillarum* Philippi included *Penicillus* (Ogden et al., 1973; Ogden, 1976) and *Halimeda* (Ogden, 1976). Feeding preferences of sea urchins

have been summarized by Lawrence (1975) and studied by Vadas (1977), Larson et al. (1980), and Vadas et al. (in press).

Of the Chlorophyta in fish-feeding trials, Earle (1972) observed that *Codium* and *Halimeda* were rapidly consumed, only portions of *Caulerpa* and *Udotea* were eaten, and *Penicillus* and *Avrainvillea* were largely not eaten. Similarly, Mathieson et al. (1975) found that *Avrainvillea nigricans* Descaisne was mostly not eaten, that most fish, except the parrotfish, did not eat *Halimeda*, that only the Grey Angelfish consumed *Caulerpa*, and that *Penicillus capitatus* and *Udotea conglutinata* remained uneaten at the end of their feeding trials. Tsuda and Bryan (1973) noted that the siganid fishes readily consumed *Caulerpa* during feeding trials. It is difficult to generalize about tropical herbivores and their feeding habits and preferences on the basis of such scant information. Of the greens we studied, however, most are apparently not eaten by many herbivores in habitat.

A few herbivores apparently can physiologically cope with, or perhaps even selectively eat, algae having chemical defenses. Sacoglossan opisthobranchs are a notable exception to the general avoidance of *Caulerpa* and members of the Codiaceae as a food source. In fact, bivalved sacoglossans are restricted to *Caulerpa*, while non-shelled sacoglossans have been reported in association with a variety of algae that include several species of Codiaceae (MacNae, 1954), and a few other Chlorophyta and *Vaucheria* (Chrysophyta) (see Kay, 1968).

The association between these algae and sacoglossans in the Caribbean has been reported from Puerto Rico (Warmke and Almodóvar, 1963), and in the Pacific from Japan (Hamatani, 1972) and Fiji (Burn, 1966). The distribution of sacoglossans appears dependent on the range of their food source, *Caulerpa* (Burn, 1966), with members of the family Juliidae reflecting the distribution of *Caulerpa* throughout the Indo-West Pacific, the Caribbean, the Mediterranean and Victoria, Australia (Kay, 1968).

Specialist herbivores were relatively common at Carrie Bow Cay. Found on *Caulerpa racemosa*

were shelled sacoglossans, *Lobiger souverbeii* (Fischer) and *Oxynoe* species, and the non-shelled sacoglossans, *Elysia cauzae* (Er. Marcus), *Elysia* species, and *Volvatella* species (the latter two and the *Oxynoe* may represent undescribed species, J. R. Lance, pers. comm.).

Some sacoglossans not only ingest intact chloroplasts from *Caulerpa* and utilize their products (see Taylor, 1968; Greene, 1974; Trench, 1975), but ingest some of the alga's secondary metabolites as well. Caulerpincin and caulerpin were identified from *Elysia panamensis* Pilsbry and Olsson (Doty and Aguilar-Santos, 1970) collected off Baja California feeding on *Caulerpa sertularioides*. This sacoglossan can secrete a milky mucus that is toxic to fish (Lewin, 1970). The biological activity of caulerpin (Figures 181a, compound I) and caulerpincin (Doty and Aguilar-Santos, 1966) was reported by Doty and Aguilar-Santos (1970) to be toxic to, and physiologically active in, mice and rats, respectively.

While *Caulerpa*, *Halimeda*, *Udotea*, *Penicillus*, *Rhipocephalus*, and *Avrainvillea* have evolved secondary compounds that deter a wide variety of herbivores, the sacoglossans have evolved a physiological mechanism for tolerating the chemical deterrents produced by the algae, and thus have become "specialists" feeding on a restricted but exclusive diet. It also appears that these specialists deter predation upon themselves by concentrating these compounds. More than three times the amount of caulerpincin and more than twice the amount of caulerpin were found concentrated in the sacoglossan *Elysia panamensis* than were found in the algal host, *Caulerpa* (Doty and Aguilar-Santos, 1970).

**PHAEOPHYTA.**—The abundant brown algae at Carrie Bow Cay belong to two families, the Sargassaceae and the Dictyotaceae. Species of *Sargassum* and *Turbinaria* (Sargassaceae) are apparently not eaten by some herbivores, at least in areas where these browns are common.

In the Caribbean, *Sargassum* and *Turbinaria* sometimes grow in areas of the reef where herbivores may have difficulty reaching them or remaining attached to feed. Also, in preliminary

subtidal feeding trials and translocation experiments of *Sargassum* in Caribbean Panama (J. Cubit and M. Hay, pers. comm.) and Islas San Blas (J. Cubit, pers. comm.), these algae were readily consumed, particularly by kyphosid fishes. These observations suggest that herbivory may limit the lower level of distribution of certain *Sargassum* species. It is also possible that increased predation or other factors may keep these fish from the reef where *Sargassum* grows; we also suggest that members of this family may not be eaten owing to their inherent high concentrations of polyphenolic substances based upon the polymerization of phloroglucinol (Figure 181c, compound IV). Types of biological activity shown by polyphenols include antibacterial (Conover and Sieburth, 1964) and antilarval (Conover and Sieburth, 1966). These polyphenols may also be ecologically important in plant-plant interactions; growth of certain phytoplankton and macroalgae may be inhibited (McLachlan and Craige, 1964) or enhanced (Ragan et al., 1980) by polyphenols.

The presence and absence of these compounds in the Sargassaceae have been reviewed by Glombitza (1977). Pfeffer (1963) suggested that the inability of fish to digest *Sargassum* was due to its tannins (Ogino, 1963). From stomach analysis of tropical reef fish, Randall (1967) concluded *Sargassum* was eaten only by a few larger herbivorous and omnivorous fishes—*Kyphosus incisor* (Cuvier and Valenciennes), *K. sectatrix* (Linnaeus), *Pomacanthus arcuatus* (Linnaeus), *P. para* (Bloch), and *Melichthys niger* (Bloch)—and that these kyphosids and *M. niger* feed on drifting algae. Earle (1972) suggested it may be eaten by certain fishes, and W. H. Adey (pers. comm.) reports that the buck-tooth parrotfish, *Sparisoma radians* (Cuvier and Valenciennes), readily consumes *Sargassum*. Atkinson et al. (1973) found that *Sargassum*, though available, was not present in the guts of *Diadema antillarum* (see also Lawrence, 1975), while another sea urchin, *Paracentrotus lividus* (Lamarck) has been recorded as feeding on *Sargassum* (Lawrence, 1975). Sammarco et al. (1974) observed lush growth of *Tubinaria* on a patch reef after they

removed *Diadema*; a diet of *Tubinaria* also provided the best growth for *Tripneustes* of the algae tested in St. Croix (J. Ogden, R. Vadas, and S. Miller, pers. comm.).

The common browns at Carrie Bow Cay belong to the Dictyotaceae; members of *Dictyota*, *Dictyopteris*, *Lobophora*, *Padina*, and *Stylopodium* are represented. Although *Padina* and *Lobophora* species are not noticeably grazed in the vicinity of Carrie Bow Cay, we have not found in them the unusual organic compounds that are present in other tropical members of the family; therefore, structure or some other factor may be important, such as increased predation upon potential herbivores, or possibly water soluble compounds or secondary compounds below our level of detection may be present. Interestingly, a Pacific species of *Lobophora* from Palau was found to contain unusual compounds (Fenical, in progress).

Of the several species of *Dictyota* occurring in the vicinity of Carrie Bow Cay (Norris and Bucher, herein: 167), we investigated the most predominant one, *D. bartayresii*, which grows among corals in the spur and groove area of the barrier reef. Recognized in the field by its marked iridescence, *D. bartayresii* in our chemical studies was shown to contain a series of toxic bicyclic diterpenoids, the major component being the compound pachydictyol A (Figure 181d, compound V), previously described by Hirschfeld et al. (1973) from another Dictyotaceae genus, *Pachydictyon* (for review of Dictyotaceae diterpenoid synthesis see McEnroe et al., 1977). Although some sea urchins have been noted to feed on some species of *Dictyota* (Atkinson et al., 1973; Abbott et al., 1974; Lawrence, 1975), as yet none are known to feed specifically on *D. bartayresii*. This alga has been recorded in stomach contents of three species of fish (Randall, 1967; Earle, 1972). It is also possible that pachydictyol A may not function to deter urchin or fish predators, but might be an example of a compound that acts against certain micro-organisms. This metabolite's toxicity to certain fungi suggests it could be defense against microbial pathogens (Fenical, unpublished data).

Another predominant brown alga at Carrie Bow Cay is *Stylopodium zonale*, which grows primarily in open, shallow areas (4–10 m depths) where it is accessible to grazers. Frequently to 20 cm in length and conspicuous in its environment, *S. zonale* is apparently not eaten by most herbivores. When freshly collected *S. zonale* is placed in cool seawater for 10 hours, the water becomes dark brown, apparently from release of pigments and secondary compounds. These substances were toxic to the herbivorous damsel fish, *Eupomacentrus leucostictus*, found at Carrie Bow Cay, and exhibited antimicrobial activity in preliminary testing. Ethanol extracts of *S. zonale* were equally toxic to damsel fish at levels of approximately 3 µg/ml. The toxic components have been found to consist of a mixture of several related C<sub>27</sub> compounds derived from a mixed biosynthesis of diterpenoid and acetate precursors. One of these compounds, the triol stypotriol (Figure 181e, compound VI), has been isolated and structurally defined (Gerwick and Fenical, 1980). We are not aware of published records of *S. zonale* as a food source for fishes or urchins. As in the green alga-sacoglossan relationship, certain mollusks may have co-evolved as specialist predators of *S. zonale*. Recent collections of this alga from the Florida Keys contained large numbers of the sea hare *Petalifera petalifera* Ranger (Fenical, unpublished data), but it was not observed on any other algae and may represent another specialist with a preferred or exclusive food source.

**RHODOPHYTA.**—Although they have the largest number of species in the environs of Carrie Bow Cay, the red algae are generally smaller in size and individual species are less abundant than either the green or brown algal species. Red algae that are apparently avoided by herbivores at Carrie Bow Cay belong to four families: *Helminthocladiaeae*, *Bonnemaisoniaceae*, *Rhizophyllidaceae*, and *Rhodomelaceae*. Members of the latter three families are known to produce elaborate halogenated, often toxic, metabolites (Fenical, 1975). With the recent discovery of unique compounds in *Liagora farinosa* (Paul and Fenical, 1980), the *Helminthocladiaeae* was

added to the expanding list of families known to produce secondary compounds.

The moderately calcified red, *Liagora farinosa* (*Helminthocladiaeae*), was seasonally abundant in the spur and groove habitats of the barrier reef at Carrie Bow Cay. We noted unusual compounds present on TLC plates, and recently Paul and Fenical (1980) described the major metabolite, an unusual acetylene containing lipid (Figure 181f, compound VII), which occurs along with several minor, related compounds in this species. These compounds were observed to be toxic against *Eupomacentrus leucostictus* at the 5–8 µg/ml range in seawater. We did not observe any grazers on *L. farinosa*.

Despite its fine, delicate structure, *Asparagopsis taxiformis* (*Bonnemaisoniaceae*) does not seem to be utilized as a food source. *Asparagopsis* species produce unique toxins, the major metabolite being the noxious compound bromoform (Figure 181g, compound VIII) (McConnell and Fenical, 1976). Several halogenated acetones are also produced by *A. taxiformis* (compounds of this type have been produced synthetically and used as tear gas).

*Asparagopsis* was not eaten by the fish *Acanthurus triostegus* (Linnaeus) (Randall, 1961), nor has it been reported as being grazed by sea urchins (Lawrence, 1975). We suggest it is not eaten by most herbivores because of its toxic metabolites. These compounds inhibited the growth of all micro-organisms tested, and they were severe lacrymators. Interestingly, though toxic or unpalatable to most grazers, it is consumed by man, for *Asparagopsis taxiformis* is the favorite seaweed food of the Hawaiians (Abbott and Williamson, 1974).

*Falkenburgia hillebrandii* (Ardissone) Falkenberg, the alternate sporophytic stage in the life history of *Asparagopsis taxiformis* (Chihara, 1961), has also been collected at Carrie Bow Cay. This morphologically different stage also appears to be avoided by grazers. In other studies, McConnell and Fenical (unpublished data) have found *Falkenburgia* from the North Atlantic also to contain bromoform. We suspect that the Carrie Bow Cay *Falkenburgia*, which is generally not eaten by herbi-

vores, also produces this compound. Fish have not been observed to feed on this stage of *Asparagopsis* (Earle, 1972), but it was found in 1% of *Diadema antillarum* guts by Atkinson et al. (1973). Since that was such a small sample, it may have indirectly been consumed while feeding primarily on other turf-forming algae. This possibility, however, will have to be further investigated.

Another red alga containing toxic secondary compounds is *Ochtodes secundiramea* of the Rhizophyllidaceae. *Ochtodes secundiramea* grows in shallow water inside the reef crest at South Water Cay, in areas of strong wave agitation and surge. This alga contains one major and one minor polyhalogenated monoterpenoid, octodene and ochtidial (Figure 181*h*, compounds IX and X) (McConnell and Fenical, 1978). Compound IX, the major metabolite, is strongly antibiotic and made up over 50% of the total organic extract of the alga. During our field studies on freshly collected specimens, we observed iridescence from the large "glandular cells" or "Drüsenzellen" (Kylin, 1956) present in the cortex of *O. secundiramea* (Joly and Ugadim, 1966). Whether these refractive bodies are the site of halogenation in *O. secundiramea* is uncertain, although we observed these bodies were no longer iridescent after the methanol extraction and they appeared to be "empty" on examination with a Wild M5 stereomicroscope. We are not aware of any published accounts of *Ochtodes* as a food source; we did not find it being grazed during our daytime observations in Belize.

Three species of the cosmopolitan genus *Laurencia* (Rhodomelaceae) from Carrie Bow Cay contained interesting secondary metabolites. This genus is known to produce a complex variety of halogen-containing compounds (Fenical and Norris, 1975; Fenical, 1975). We conducted chemical studies on the two abundant species, *Laurencia caraibica* and *L. obtusa* (identified following Taylor, 1960:626), at Carrie Bow Cay. The third species, *L. intricata* Lamouroux, was not abundant enough for further study, even though an initial TLC indicated the presence of secondary compounds.

*Laurencia caraibica* Silva grows sympatrically

with *L. obtusa* in areas of intense water motion, generally along the outer reef crest. This alga produces quantities of the antibiotic cuparane derivative allolaurinterol (Figure 181*i*, compound XI), a compound which has also been isolated as a minor component of *L. subopposita* (J. Agardh) Setchell from California (Wratten and Faulkner, 1977) and *L. filiformis* (C. Agardh) Montagne from the east coast of Australia (Kazlauskas et al., 1976). Izac and Sims (1979) discovered a unique iodinated sesquiterpene in *L. caraibica*, the first report of such a compound and of iodine being found in the genus. We found the same major metabolite in this species, and did not observe this alga being eaten by fish or urchins.

*Laurencia obtusa* was found in large quantities along the Carrie Bow Cay reef crest (at least during April and May). We found this alga to contain more than 3% (dry weight) of the cytotoxic chamigrene derivative elatol (Figure 182, compound XII), a compound originally isolated from the Australian species *L. elata* (C. Agardh) Hooker and Harvey (Sims et al., 1974). Elatol has subsequently been found to be moderately antibiotic, but more interestingly this compound shows exceptional toxicity against fertilized sea urchin eggs, and totally inhibits cell division (Fig-

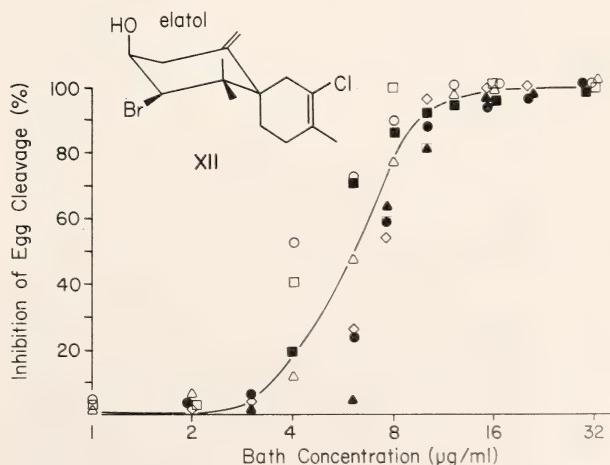


FIGURE 182.—Dose-response curve of elatol (compound XII) from *Laurencia obtusa*, against fertilized eggs of the sea urchin, *Strongylocentrotus purpuratus* (the seven markers represent individual experiments).

ure 182). The dose-response curve of elatol with fertilized eggs from *Strongylocentrotus purpuratus* (Stimpson), a California urchin, shown in Figure 182, has been provided by R. Jacobs. The LD<sub>50</sub> of elatol is estimated at about 7 µg/ml bath concentration. *Laurencia obtusa* is not grazed by *Diadema* (Ogden, 1976), and is avoided by most herbivores. It is interesting to speculate on the ecological role of compounds such as elatol, which are now known to inhibit, or, at certain levels, to kill developing sea urchin eggs. We hypothesize that if such compounds are released or secreted in the vicinity of *Laurencia* stands, they could inhibit sea urchin egg development in situ, and thus give the alga a selective advantage against the settlement and development of potential predators in their vicinity.

In view of the biologically active constituents from *Laurencia*, it is not surprising that the alga has few predators. The sea hares (Anaspidea), particularly some species of *Aplysia*, have specific feeding preferences for *Laurencia*. In our field studies in the Gulf of California, California, the Galápagos Islands and now in Belize, we have observed this grazer-alga relationship between *Laurencia* and *Aplysia*. During our spring studies at Carrie Bow Cay, we typically found *A. dactylomela* (Ranger) grazing on *L. obtusa* on the fore-reef crest. It appears that some *Aplysia* species may be dependent on *Laurencia*, at least during certain stages of their life cycle, as larvae and juveniles. Culture studies on *A. californica* Cooper (Kriegstein et al., 1974) indicate that settling and metamorphosis of the free-swimming larval stage are enhanced by the presence of *Laurencia pacifica*.

Stallard and Faulkner (1974) showed that *Aplysia californica* concentrated the metabolites of *Laurencia pacifica* in their digestive glands. We have found quantities of elatol, identified from *L. obtusa* in our study, in the digestive glands of *A. dactylomela*. It has been proposed that the concentration of the algal metabolites by the sea hare provide a selective advantage against potential predators (Stallard and Faulkner, 1974; Kittredge et al., 1974). Although the defense role of this concentration needs to be tested, known predators of *Aplysia* are few, and opisthobranchs in general are avoided as a food source by Caribbean fish (Ran-

dall, 1967). Opisthobranch gastropods used in feeding-acceptability tests with selected fish by Thompson (1960) were almost invariably refused.

Recently, it was suggested that juveniles of the tropical bridled burrfish, *Chilomycterus antennatus* (Cuvier), in Caribbean Panama, are Batesian mimics of *Aplysia dactylomela* and perhaps avoid predation by mimicking the shape and coloration of the "unpalatable sea hare" (Heck and Weinstein, 1978). We suggest that the avoidance could be due to the concentration of elatol by *A. dactylomela* from *Laurencia obtusa*.

### Summary and Conclusions

Our studies of Belize macro-algae, indicate that members of specific algal families—the Caulerpaceae, Codiaceae, Udoteaceae, Dictyotaceae, Sargassaceae, Helminthocladiaeae, Bonnemaisoniaceae, Rhizophyllidaceae, and Rhodomelaceae—produce unusual secondary compounds. The species we studied are not eaten by many herbivorous fishes or sea urchins. These herbivores and the coral reef algae on which they feed appear to represent a co-evolved system of defense and counterdefense. Chemical defense appears successfully to deter the majority of herbivores; however, some specialist grazers have co-evolved physiological mechanisms that enable them to tolerate or possibly even select for some of these same algae. In some specific animal-plant interactions, for example, saccoglossan-*Caulerpa* and *Aplysia-Laurencia*, the mollusks not only exclusively select certain algal species for food and show preference for others but they also concentrate the alga's secondary compounds as defense against being preyed upon. Thus, it appears the chemical deterrent against most herbivores may have become a chemical attractant to these specialist species. Published evidence and our own observations, though scant, indicate most herbivorous reef fishes are highly selective in the algae they consume. In tropical reef algal-animal relationships, there is strong evolutionary interaction between herbivores and algae, based on the alga's defenses—structure (Lubchenco, 1978), productivity and growth form (Littler, 1980), life history strategy (Lubchenco and Cubit, 1980), habitat,

and chemistry—and the herbivore's feeding habits (preference for, or not eating of, algae and the peculiarities of their digestive physiology).

Ehrlich and Raven (1965) first attributed to secondary compounds of plants a key role in determining the pattern of insect-plant co-evolution. As suggested by Feeny (1975), we may be witnessing an "evolutionary arms race" in which the algae must deploy part of their metabolic budget on defense against herbivory, and the herbivores must devote a portion of their assimilated energy on ways to locate their algal food, know which species to avoid, and on developing counter measures to tolerate the alga's chemical

defense (see for example feeding preference studies of Vadas, 1977; Larson et al., 1980; for additional interpretation of "evolutionary arms race" theory, see Atsatt and O'Dowd, 1976).

The subject of tropical reef algal-animal interactions presents a myriad of problems to be investigated and questions to be answered. Recognizing the speculative nature of this study we concur with Janzen (1977) that there is "quite enough hypothetical biology on the books" and we now need quantitative ecological and behavioral studies "on the pragmatics" of tropical plant-animal interactions.

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# Life History of the Hydromedusa *Stomotoca pterophylla* Haeckel and Its Ichthyoparasitic Hydroid

Ronald J. Larson

## ABSTRACT

Hydroids of the genus *Hydrichthys* Fewkes, 1887, were found parasitizing about 30% of the leptocephalid fish larvae collected at night from a shallow reef flat at Belize, Central America. Little or no specificity was shown for either host or site of attachment. Medusae released from these hydroids and reared in the laboratory for a period of three weeks were identified as *Stomotoca pterophylla* Haeckel, 1879. The hydroid stage of this medusa was hitherto unknown. Because *S. pterophylla* medusae are epipelagic, the leptocephalids probably were parasitized in the open ocean rather than near shore. The generic name *Stomotoca* L. Agassiz, 1862, predates *Hydrichthys* Fewkes, 1887, and therefore has taxonomic priority. Hydroids of *Hydrichthys* (= *Stomotoca*) species are highly variable in their morphology. As a result, it is doubtful that all of the five previously described species are valid.

## Introduction

Hydroids are known to occur on a wide variety of substrates, including plants and animals. Fewkes (1887) described *Hydrichthys mirus* attached to *Seriola zonata* (Cuvier), a teleost fish. Since the hydranths lacked tentacles, Fewkes (1888) suspected that the hydroid might be a true parasite. Later, Warren (1916) reported another species of *Hydrichthys*, *H. boycei*, and substantiated

its suspected parasitic habits by noting that its polyps fed on the dermis of fish. The worldwide appearance on a variety of host fishes has been described for three additional species of this genus. Because of the parasitic specializations and highly variable morphology of the hydroids, in addition to our lack of knowledge concerning the medusae of the genus *Hydrichthys* Fewkes, 1887, (= *Stomotoca* L. Agassiz, 1862) the systematic position and the validity of *Hydrichthys* spp. are obscure. This paper is the first description of the life cycle of *Stomotoca pterophylla* Haeckel, 1879. Aspects of its unique life history and the taxonomy of "Hydrichthys" (= *Stomotoca*) spp. hydroids are discussed.

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## Materials and Methods

Hydroids and medusae were collected at Carrie Bow Cay, located on the barrier reef of Belize, Central America, in March and April 1977 and 1978, and November 1978. Medusae and leptocephalus larvae with attached hydroids were obtained by suspending a 30 cm diameter, 220 µm mesh plankton net, at night, from a pier over the reef flat and allowing water currents to carry the specimens into the net. Water depth here varies from 0 to 0.5 m; the bottom consists of coral

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rubble, living coral, coarse *Halimeda* spp., sand, and *Thalassia testudinum* Banks ex König. About 0.6 km seaward of Carrie Bow Cay is the shelf edge, where water depth reaches more than three hundred meters.

Newly released medusae were obtained by placing leptocephali with hydroids in small bowls of sea water overnight. These medusae were kept in bowls; the sea water was changed at least once daily, generally after feeding. For feeding, medusae were transferred, via pipette, to watch glasses. When possible, each specimen was individually fed to repletion once or twice daily. Initially, medusae were fed boiled egg yolk and *Artemia salina* (Linnaeus) nauplii; after one week, small pieces of gonad from the echinoid *Lytechinus variegatus* (Lamarck) and bits of lobster and fish muscle were used. The third week, the diet consisted of live medusae, *Liriope* sp. and *Phialidium* sp., and chaetognaths.

All material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

## Results

Leptocephali were found only at night on the reef flat. During each 30-minute plankton tow, 10 to 20 or more larvae were collected. The larvae had an adult-like head indicating an advanced stage (Figure 183d) and when kept in the laboratory they metamorphosed into juveniles after three to 14 days.

Hydroid colonies were found on a significant number of leptocephalids. Of 101 larvae examined, 35 had attached hydroid colonies. In all, 10 species of larvae were collected: *Ahlia egmontis* (Jordan), *Myrophis punctatus* Lütken, *Myrophis platyrhynchus* Breder, *Albula vulpes* Linnaeus, *Arisoma baleanicum* (De la Roche), *Chilorhinus suensoni* Lütken, *Moringula edwardsi* (Jordan and Bollman), *Elops saurus* Linnaeus, *Ophichthus* sp., and ?Ophichthidae; only the first four species mentioned were parasitized by hydroids. *Ahlia egmontis* and *M. punctatus* were the most abundant in the collections and also accounted for the majority of the hydroid colonies. Since most of the other six

species were represented by only one or two specimens, the degree of parasitism could not be determined. By contrast, *C. suensoni* was represented by eight specimens that were all free from infection, indicating that this species may be able to avoid the hydroid.

The presence of hydroids on all areas of the body points to a lack of specificity for attachment sites. Generally, only a single colony was found per fish; however, several had two, and one had four on different areas of the fish.

**LIFE HISTORY OF *Stomotoca pterophylla* HAECKEL.**—*Description of Polyps:* Hydranths protrude from naked basal anastomotic hydrorhizal plates, 1 to 4 mm in diameter, that are attached to the dermis of the eel larvae (Figure 183d). Polyps are elongate, 0.5 to 4.0 mm in length, without tentacles, and number 10 to 20 or more per colony. Medusae buds occur on nearly every colony but their number and location depend on the polyp size. Twenty five or more occur over most of the lateral branches of the large, 2 to 4 mm long, hydranths (Figure 183c). Smaller polyps, 0.5 to 2.0 mm, on the proximal portion of the hydranth generally show few sessile buds (Figure 183a,b). Medusae buds first appear as globular outgrowths from the polyps, later elongating and then developing a pair of triangular tentacle rudiments. In life, polyps are reddish, medusa buds are unpigmented except for the yellowish endodermal region of the manubrium and the tentacle rudiments. From these characters the hydroids are identified as belonging to the genus *Hydrichthys* Fewkes, 1887.

*Description of Medusae:* The bell-shaped umbrella of medusae reared from *Hydrichthys* sp. polyps measures 0.5 to 0.7 mm in height and is slightly narrower than tall (Figure 184a). Cnidae are scattered over the exumbrella. The cruciform manubrium occupies about one-half the diameter of the subumbrellar cavity. Lips are simple, not folded. Two opposite tentacles originate from flattened triangular perradial marginal bulbs. Two remaining perradial bulbs are wart-like and without tentacles. Four smaller wart-like bulbs occur interradially. Vascular canals are narrow. The gastrodermis of the manubrium and the

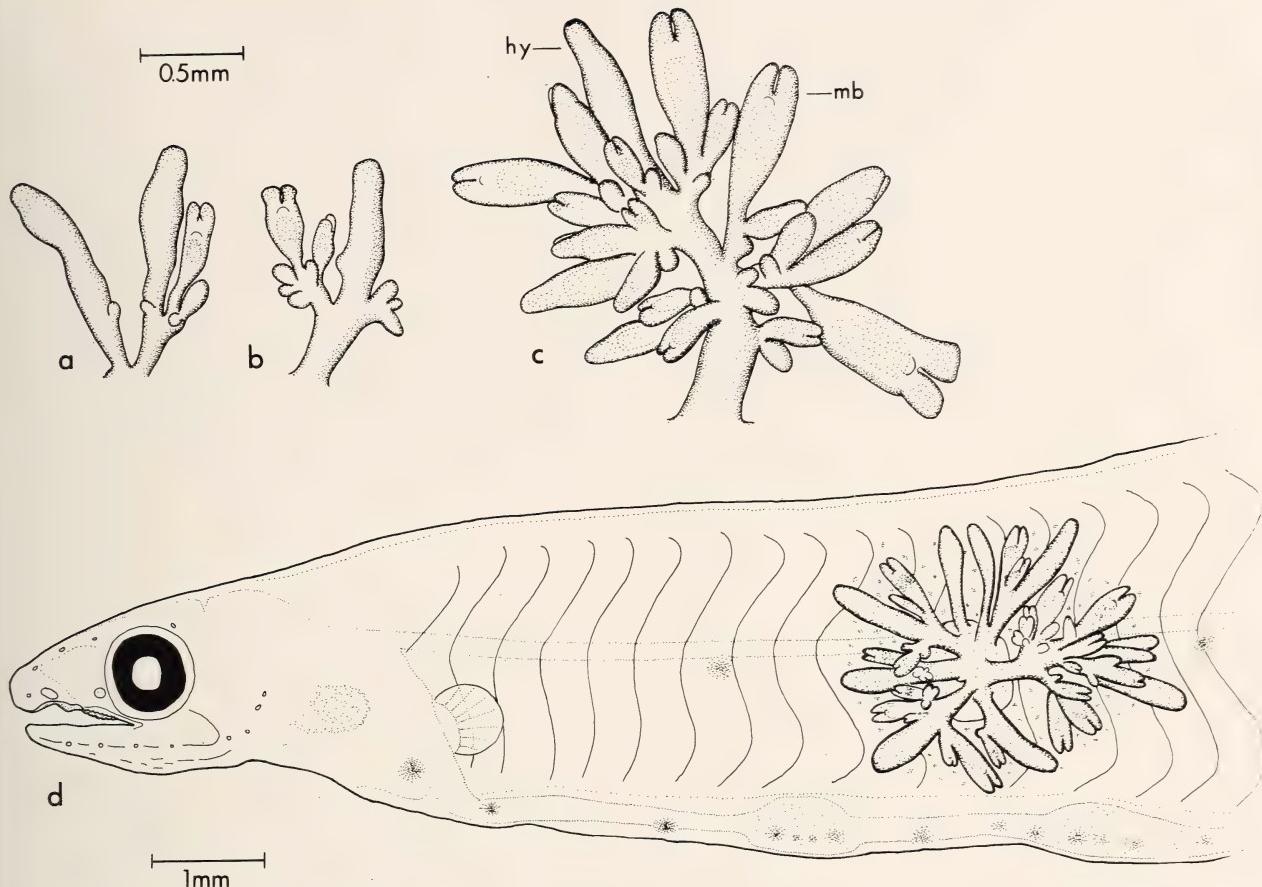


FIGURE 183.—*Stomotoca pterophylla* hydroids: a-c, hydranths with developing medusa buds (a,b with several buds, c with numerous buds); d, metamorphosizing leptocephalid *Myrophis punctatus* with *S. pterophylla* hydroid colony attached to left side (hy = hydranth, mb = medusa bud).

marginal bulbs is reddish-orange in color, other structures are unpigmented.

Newly released *Stomotoca pterophylla* medusae collected directly from the reef flat are morphologically identical to those released in the laboratory. During subsequent growth, the most notable changes are the appearance of an apical projection, absolute and relative increase in manubrium length, formation of gonads, and increase in the number of marginal warts. At 3 mm bell height (7 days), the umbrella develops an apical projection (Figure 184b), the manubrium extends to the velum, and 12 to 18 marginal bulbs become evident. At 5 mm height (9-14 days) the apical projection becomes more prominent, the manubrium originates from a slight peduncle, the mouth stretches beyond the velum, the lips fold

slightly, adradial gonads appear in 2 to 5 transverse folds on the proximal portion of the manubrium, and 16 to 30 marginal warts become apparent (Figure 184c). Already at this stage the two opposite tentacles, peduncle, and folded adradial gonads are diagnostic of the genus *Stomotoca* L. Agassiz, 1862. At 8 mm bell height (14-17 days) the peduncle enlarges, and adradial gonads add folds, even secondary folds on the largest specimens (Figure 184d), and the lips also plicate. The gastrodermis of the manubrium, tentacle bulbs, and marginal warts is brownish. After 21 days of development, the total observation time, only two of the 25 specimens have bell heights of 10 mm. At this time, the bell shape appears quite variable from specimen to specimen owing to differential resorption of the mesoglea during pe-

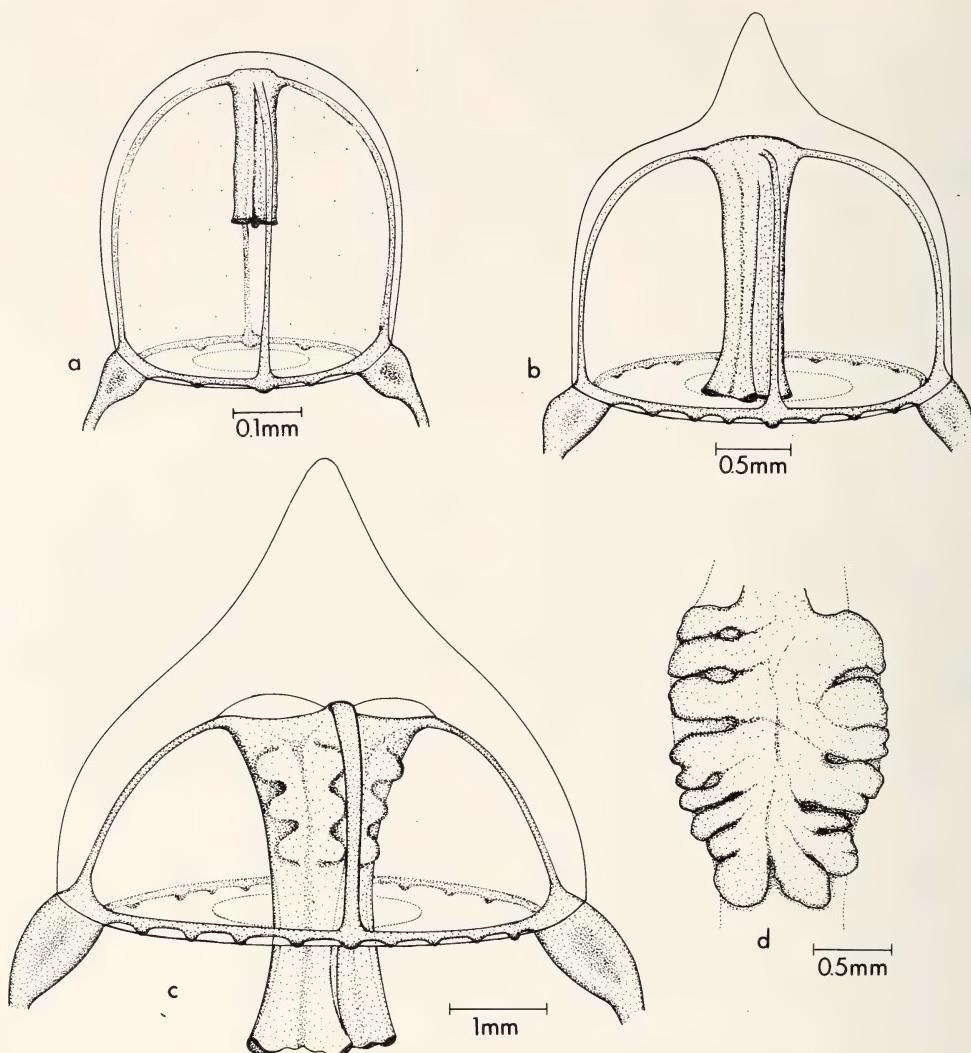


FIGURE 184.—*Stomotoca pterophylla* medusae: *a*, newly released, about 0.5 mm bell height; *b*, approximately 7 days old, about 3 mm high; *c*, approximately 14 days old, 5 mm high, gonads appear as folds on manubrium; *d*, front view of folded gonad of 17-day old, 8 mm high medusa.

riods when the medusae would not feed. Because of the presence of secondary gonad folds, these medusae are diagnosed as *Stomotoca pterophylla* Haeckel, 1879.

*Behavior of Polyps and Medusae:* Although hydranths are typically inactive, sporadic serpentine motion, bending, turning, and mouth opening were observed. During feeding, hydranths bend over touching the epidermis of the host leptocephalus, and open the mouth wide, trumpet-like, over a small area of the fish. Cnidae inside the mouth may attach the polyps's circular lip to the

larvae during feeding. Damage to surrounding fish tissues was observed in all cases, as indicated by numerous minute pits and surface irregularities surrounding the hydroid colony. Hydranths removed from their hosts were incapable of capturing live *Artemia salina* nauplii, but would eat dead nauplii.

*Stomotoca pterophylla* medusae actively pulsate except when feeding. Since the medusae lack sufficient propulsion to maintain themselves off the bottom of the observation dish, they may, in the open ocean, rely on water turbulence to help

stay adrift. The long filiform tentacles extending to 15 or more times the bell height are probably used to reduce sinking as well as to capture prey. When food is touched to one or both tentacles they contract and bend inward; the mouth is then projected outwards by contraction of the umbrella, the food is grasped by the lips, and swimming pulsations cease. In newly released medusae, it is sometimes necessary to place the food inside the umbrella cavity to produce this feeding behavior. Usually if a medusa keeps swimming, the food is dropped. Specimens that repeatedly reject food show signs of starvation, that is, resorption of umbrellar mesoglea.

### Discussion

Previously, the hydroid stages of *Stomotoca* spp. were unknown. Strong (1925) obtained planulae from *Stomotoca atra* L. Agassiz medusae from Puget Sound. These planulae failed to settle even though a variety of substrates was offered; Strong suggested that the hydroid might be substrate specific. Because *S. atra* and *S. pterophylla* medusae are taxonomically separated on only a few minor criteria (see Bigelow, 1909), undoubtedly their hydroid generations are similar. Thus the hydroid stage of *S. atra* probably occurs parasitically on fishes. Strong (1925) also found in the Puget

Sound region a hydroid of the family Pandeidae, *Perigonimus repens* (Wright) commonly attached to the marine fish *Hypsagonus quadricornis* Cuvier and Valenciennes. Although the medusa stage for *P. repens* is unknown, it is unlikely that this is the hydroid of *S. atra* medusae because it is morphologically very different from the hydroid of *S. pterophylla*.

Table 33 lists the host fishes on which "Hydrichthys" spp. and *Ichthyocodium sarcotretis* Jungersten, a closely related species, have been reported. Many of these species, for instance, *Cyclothona signata* Garman, *Ceratias holboelli* Krøyer, *Diaphus theta* Eigenmann and Eigenmann, *Lampanyctus leucopsarus* (Eigenmann and Eigenmann), *Tarletonbeania crenularis* (Jordan and Gilbert), and *Benthosema glacialis* (Reinhart), are pelagic. Others have long-lived larvae, like *Acanthurus triostegus sandvicensis* Streets, which was found to be planktonic for 2 1/2 months (Randall, 1961).

*Myrophis punctatus*, the most heavily parasitized leptocephalid found during this study, has a pelagic larva that lives offshore for as long as 6 to 14 months before moving inshore and metamorphosing (M. Leiby, pers. comm., 1979). This long pelagic life may be the reason why it is parasitized more often than benthic or inshore species without pelagic larvae, in light of the medusa stages of the hydroids also being pelagic.

TABLE 33.—Previous reports of the hydroids "Hydrichthys" and *Ichthyocodium*, and their host fishes

Hydroid	Host fish	Reference
<i>Hydrichthys boycei</i> Warren	<i>Ambassis safgha</i> (Forskål) <i>Chaetodon lunula</i> (Lacépède) <i>Mugil</i> sp.	Warren, 1916; Millard, 1975
<i>Hydrichthys cyclothonis</i> Damas	<i>Cyclothona signata</i> Garman	Damas, 1934
<i>Hydrichthys mirus</i> Fewkes	<i>Seriola zonata</i> (Cuvier)	Fewkes, 1887
<i>Hydrichthys pacificus</i> Miyashita	<i>Acanthurus triostegus sandvicensis</i> Streets	Randall, 1961
<i>Hydrichthys pietschi</i> Martin	<i>Chaetodon</i> sp.	Miyashita, 1941
<i>Hydrichthys</i> sp.	<i>Ceratias holboelli</i> Krøyer	Martin, 1975
	<i>Diaphus theta</i> Eigenmann and Eigenmann	McCormick et al., 1967
	<i>Lampanyctus leucopsarus</i> (Eigenmann and Eigenmann)	
	<i>Tarletonbeania crenularis</i> (Jordan and Gilbert)	
	<i>Benthosema glacialis</i> (Reinhart)	Jungersen, 1911
<i>Ichthyocodium sarcotretis</i> Jungersen	<i>Sebastes mentella</i> Travin	Templeman, 1973
? <i>Ichthyocodium sarcotretis</i> Jungersen	? <i>Sebastes fasciatus</i> Storer <i>Sebastes mentella</i> Travin	Jones, 1966

In the Atlantic, most *Stomotoca pterophylla* medusae have been collected in oceanic regions—the Florida current, Gulf Stream, and in the mid-Atlantic (see Kramp, 1959)—rather than in neritic waters. At Carrie Bow Cay, numerous juvenile *S. pterophylla* medusae were collected, but no mature specimens were found. Hence it is probable that the leptocephali captured at Carrie Bow Cay were parasitized during their lengthy larval period in the open ocean.

In conjunction with showing the genera *Hydrichthys* and *Stomotoca* to be synonymous, it is essential to determine the taxonomic status of the species in *Hydrichthys*. Unfortunately, hydroids in this genus are separated on the basis of highly variable morphological characters, for instance, height and diameter of colony, extent of branching, and location of medusa buds. Rather than being genetic, these criteria probably depend on size of host, age of colony, and other ontogenetic factors. The genus *Ichthyocodium* Jungersen is morphologically similar to the genus *Hydrichthys*, which was also described on the basis of characters that are likely to be affected ontogenetically. Since the hydroids of the genera *Hydrichthys* and *Ichthyocodium* are specialized, owing to their parasitic existence, they have few morphological characters, which seem to vary with environmental conditions. Consequently, it may be impossible to separate members of these genera solely on polyp morphology. Host specificity may also be of limited taxonomic value, since this study shows that many hosts are parasitized. Although *Ichthyocodium sarcotretis* seems to parasitize only ichthyoparasitic copepods, McCormick et al. (1967) found *Hydrichthys* sp. attached to both copepods and fish. They, too, suggested that host specificity may not be taxonomically useful.

Comparison of medusae from these species may

prove to be the most reliable means of identification. Where known, the medusae buds of all species of *Hydrichthys* and *Ichthyocodium sarcotretis* are similar (Fewkes, 1888; Jungersen, 1911; Warren, 1916; Damas, 1934; Miyashita, 1941; Jones, 1966; McCormick et al., 1967; Templeman, 1973). Juvenile medusae are known for only two species of these hydroids, *H. mirus* and *H. boycei*. Fewkes (1888) reported that the juvenile medusa of *H. mirus* has a cruciform manubrium and two tentacles, but that it later develops a circular manubrium and four tentacles. This report led Mayer (1910) to postulate that this medusa might belong to the genus *Sarsia*. Warren (1916) found that the juvenile *H. boycei* medusa resembles newly released *H. mirus* but, doubting that it could develop more tentacles, he separated the two species. The fully developed medusa of *H. mirus* is different in many respects from the medusa of *Stomotoca pterophylla* reported herein. It is possible that Fewkes accidentally introduced *Sarsia* sp. medusae into his cultures and mistook them for the advanced medusae of *H. mirus*.

Clearly, much confusion exists about the validity of hydroids referred to the genus *Hydrichthys*. The true identity of those supposed species awaits examination of their life histories. Yet, there is little doubt that the genus *Hydrichthys* Fewkes, 1887, is synonymous with *Stomotoca* L. Agassiz, 1862. Accordingly, the new combinations are as follows: *Hydrichthys boycei* Warren, 1916 = *Stomotoca boycei* (Warren, 1916); *Hydrichthys cyclothonis* Damas, 1934 = *Stomotoca cyclothona* (Damas, 1934); *Hydrichthys mirus* Fewkes, 1887 = *Stomotoca mira* (Fewkes, 1887); *Hydrichthys pacificus* Miyashita, 1941 = *Stomotoca pacifica* (Miyashita, 1941); *Hydrichthys pietschi* Martin, 1975 = *Stomotoca pietschi* (Martin, 1975).

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# Variation in Growth Forms of the Reef Coral *Montastrea annularis* (Ellis and Solander): A Quantitative Evaluation of Growth Response to Light Distribution Using Computer Simulation

Richard R. Graus  
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## ABSTRACT

A new computer simulation model is used to evaluate the relationship between the various growth forms of small isolated colonies of *Montastrea annularis* (Ellis and Solander) and submarine light distribution. In this model (Model 2) calcification rate as a function of light intensity is calculated from detailed measurements of skeletal growth rate and skeletal density in colonies collected from various depths off Carrie Bow Cay, Belize, and one large colony from Discovery Bay, Jamaica. A previous model (Model 1) was based on laboratory studies of photosynthesis rates and calcification in response to light intensity (Graus and Macintyre, 1976).

Although these two models represent independent approaches to the understanding of coral morphogenesis, the simulation outputs are essentially similar and replicate the morphotypic variations of *M. annularis* observed in increasing water depths off Carrie Bow Cay. These two models together corroborate the hypothesis that light intensity and distribution provide the major ecological control for the skeletal morphogenesis of *M. annularis*.

## Introduction

Numerous colonies of the Caribbean coral *Montastrea annularis* (Ellis and Solander) collected be-

tween 1972 and 1979 from various reef settings and depths at Carrie Bow Cay, Belize, have provided considerable morphological information about skeletal growth and its intraspecific variability. Colonies of *M. annularis* transplanted from shallow water to deep water and vice versa helped us to identify skeletal characteristics that are light responsive. The modification of these characteristics in the transplanted colonies and their variability among in situ colonies suggest that eco-phenotypic factors account for differences in growth form over the environmental range of this species, principally the ecophenotypic response of *M. annularis* to light. New data on light response have allowed us to propose a second model for skeletal growth that corroborates the hypothesis generated from an earlier model that was based on experiments of light-mediated photosynthesis and calcification of *M. annularis* (see Graus and Macintyre, 1976; Graus, 1977).

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## Methods

Between 1972 and 1979 colonies of *Montastrea annularis* were collected from various reef locations off Carrie Bow Cay over a depth of 0.5 to 30.0 m. Many of these colonies were stained—some annually over a period of five years—with Alizarin Red-S to provide an accurate time marker for measuring growth rate. Stain lines correlated with cyclic density bands in x-radiographs (Macintyre and Smith, 1974), which were also used to measure growth.

The effects of ambient radiance distribution on growth form were tested by transplanting colonies from shallow to deep locations on the reef and vice versa (details given in Table 34). First, however, each colony was stained with Alizarin Red-S and nails were hammered into the skeleton vertically at the crest and horizontally in the direction of North in order to establish the original orientation at the new site. The colony was removed with a hammer, cemented to a concrete block, transplanted, left for three years, and then collected.

Two-dimensional light fields were measured in the solar plane around several in situ and transplanted colonies at depths from 0.5 to 20.0 m by means of an underwater radiometer-photometer (United Detector Technology 40X Opto-Meter). Measurements were recorded on clear days at 30° intervals from 0° (up) to 180° (down), east and west of vertical, while the sun was near the zenith. Although we did not conduct a comprehensive

survey of light at other azimuths and solar altitudes, we computed an attenuation coefficient that enabled us to correlate our Belizean data with the more extensive radiance data from Curacao (Roos, 1967).

Morphological measurements were obtained from vertical skeletal slabs (approximately 0.5 cm thick) cut through the crest of each colony. The slabs were x-rayed and each negative made into a positive contact print on which morphological measurements were made directly. Consecutive dark and light density bands prominent in the x-radiographs represent annual skeletal growth in most colonies (Figure 185). Care must be taken, however, to differentiate between these pairs of bands and other bands caused by local and regional noncyclic environmental fluctuations. Skeletal growth rate was determined on the basis of the length of a corallite within a given band (since corallites normally grow perpendicular to the growth surface). This distance was measured with vernier calipers.

Skeletal growth rate is known to vary with orientation of the corallites, which can be determined by measuring the corallite growth angle. This angle is defined as the interior angle between a corallite's axis of growth and the vertical direction. We measured this angle with a straight edge and a goniometer.

Skeletal density was measured in rectangular slabs (approximately 3 × 3 × 1 cm) cut from (a) the crest and flanks of 9 specimens of *Montastrea annularis* from Carrie Bow Cay and (b) 12 posi-

TABLE 34.—Transplant conditions for colonies of *Montastrea annularis*; all at Carrie Bow Cay reef except colonies 5 and 6 (P. Dustan's 3-year transplant colonies from Jamaica); colony 8 rotated 65° at same depth

Colony number	Original depth (m)	Transplant depth (m)	Transplant location	Transplant date	Collection date
1	1	14	Outer ridge	Jun 1975	Mar 1978
2	1	14	Outer ridge	Jun 1975	Mar 1978
3	1	21	Inner-reef slope	Apr 1975	Mar 1978
4	1	21	Inner-reef slope	Apr 1975	Mar 1978
5	1	31	Fore-reef slope	Jun 1975	Mar 1978
6	45	15	Jamaica	Aug 1972	Aug 1975
7	45	15	Jamaica	Aug 1972	Aug 1975
8	1	1	Back reef	Apr 1975	Mar 1978

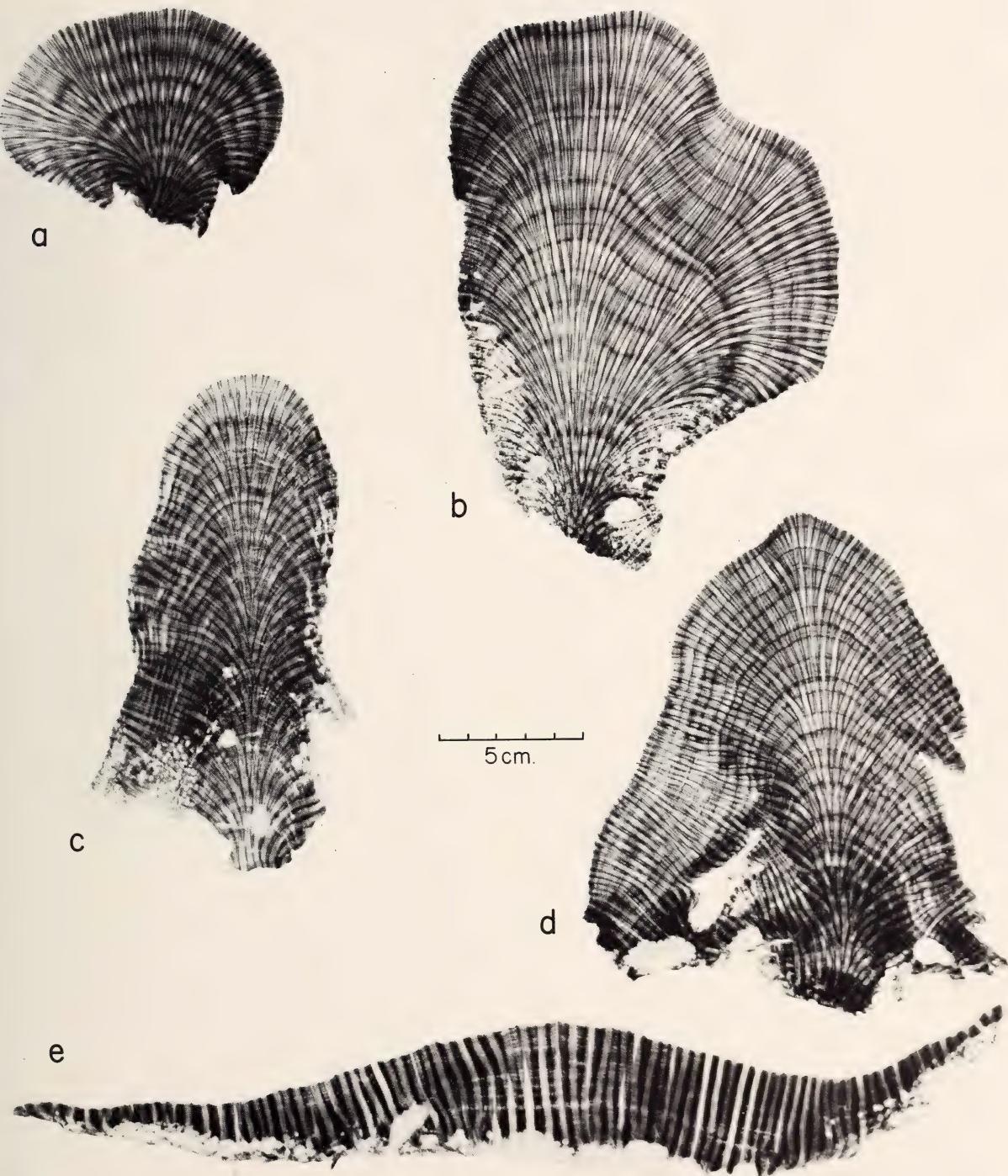


FIGURE 185—Variations of coral growth patterns of *Montastrea annularis* with respect to water depth along the Carrie Bow Cay transect as shown by the five morphotypes recognized in this study: *a*, hemisphere, 1 m; *b*, tapered hemisphere, 10 m; *c*, column, 22 m; *d*, flared column, 25 m; *e*, plate, 30 m; colonies are in life orientation, except for the plate (*e*), which originally dipped 30° to the left.

tions spanning the entire range of growth angles on a colony of *M. annularis* from a depth of 5 m off Jamaica. An analytical balance was used to weigh the slabs both in air ( $W_a$ ) and suspended in water ( $W_w$ ). The weight in water was recorded within seconds of immersion in order to minimize seepage into the skeleton. The percentage of error for this procedure was thereby kept to less than 1%. The weights in air and in water together with the density of water ( $P_l = 1.000 \text{ g/cm}^3$ ) were used to calculate skeletal density ( $P_s$ ) from Archimedes' formulas as follows:

$$P_s = P_l \cdot \frac{W_a}{(W_a - W_w)}$$

Intercorallite spacing was measured on five colonies from depths of 0.5 to 30.0 m off Carrie Bow Cay and on one colony from a depth of 5 m off Jamaica. Photographic studies were based on enlarged  $8 \times 10$  in ( $20 \times 25$  cm) prints of small sections of the surface of Carrie Bow Cay specimens, both at the crest and lower flanks of the colony. In the 30 m plate morphotype, however, sections at the center and outer edge were photographed. The specimen from Jamaica was photographed at 12 positions over the entire range of corallite growth angles. Owing to curvature of the surface of colonies, only 10 to 15 corallites at the center of each print were oriented perpendicular to the film and therefore only those could be measured without a distortion of distance. The distance between the centers of each neighboring pair of these central corallites was measured with vernier callipers.

## Results

**MORPHOLOGICAL VARIABILITY.**—The massive variety of *Montastrea annularis* has been classified into three morphotypes on the basis of variations that occur at different depths over the entire range of this species: hemispheric, 0–5 m; columnar, 5–25 m; and platy, >25 m (Macintyre and Smith, 1974; Graus and Macintyre, 1976; Graus, 1977). Our recent measurements of specimens from Carrie Bow Cay indicate that these three morphotypic stages are actually part of a contin-

uous gradient that changes with depth. This gradient is described below in terms of five colonies that reflect distinct morphotypic stages.

**Hemisphere** (Figure 185a): The colony from a depth of 1 m in the rubble and pavement zone off Carrie Bow Cay shows 10 years of growth from its fractured base. Its predominant morphological features are radiating corallites and the almost concentric, paired, high and low density bands representing annual growth. The rate of skeletal growth was found to be highest at the crest, averaging 0.83 cm/y for the life of the colony. The rate is nearly constant for angles of corallite growth up to  $60^\circ$ , but gradually diminishes thereafter and reaches 0.24 cm/yr at the maximum angle of  $141^\circ$ . This pattern repeats annually, gradually developing the form of the corallum. This growth pattern also influences the directions of corallite growth. At the crest, where the growth rate is nearly constant, all corallites except for those lying along the vertical axis radiate linearly away from each other. Because of differential growth rate along the flanks, corallites curve away from the vertical until the polyps eventually die out at the lower periphery.

Interior budding occurs in regions of greatest corallite divergence (for example, the crest and raised humps). Peripheral budding occurs along the lower flanks at the free edge of the epitheca, and thus gradually extends the flanks to the substratum.

**Tapered Hemisphere** (Figure 185b): This specimen from a depth of 10 m in the high-relief spur and groove zone resembles the hemispheric form, in its high, relatively uniform growth rate (0.93 cm/y) over the broad region of the crest. However, the maximum corallite growth angle at  $110^\circ$  is lower than that of the hemispheric form. The tapered form expands upward rapidly and outward gradually; because the maximum angle of corallite growth is greater than  $90^\circ$ , the mature form becomes a hemisphere that tapers like an inverted cone toward a smaller base.

**Column** (Figure 185c; Plate 4: center left): This specimen from a depth of 22 m on the inner-reef slope has a growth history of 24 years. Maximum skeletal growth rate at the crest averages 0.63

cm/y, which is lower than in either the hemisphere or tapered hemisphere stages. The growth rate diminishes beginning at a 10° angle of corallite growth and reaches a minimum rate of 0.18 cm/y at an angle of 95°. The high differential growth rate between the crest and flanks produces strong curvature and divergence of corallites and thus creates room for new buds. Almost all corallites in the colony originate in an area that was an earlier crest of the colony. The geometry of corallite growth paths and the shape of the entire colony are similar to the axial growth pattern of branching corals (for example, species of *Stylophora*, *Pocillopora*, *Porites*, and *Dendrogyra*). Peripheral budding at the lower flanks forms epithelial extensions of the lower flanks, or skirts that become separated from the main skeleton. Buds initially grow parallel to the surface of the skirt, but within a year or two these buds turn around to a nearly perpendicular orientation. The skirts develop a concave upward form after several years because each new generation of buds turns a few additional degrees toward the vertical. Because these buds are not locked in on all sides by other corallites, they have more freedom in their direction of growth and can thereby influence the shape and orientation of the skirt. Although the colony has become distinctly columnar after 24 years of growth, its annual bands indicate that the earliest stage was hemispherical and that the present columnar form developed gradually.

*Flared Column* (Figure 185d): This colony from 25 m indicates a maximum growth rate at the crest of 0.64 cm/y, which is similar to that of the columnar form, but here the maximum angle of corallite growth (60°) is much lower than for the columnar form. As in that form, peripheral budding in the flared column leads to the formation of skirts. The growth habit of this stage produces a broadly conical colony that is peaked at the crest and flared at the base.

*Plate* (Figure 185e): This colony from 30 m on the fore-reef slope shows 20 years of growth from the base. Although the colony's orientation is horizontal in this illustration, it was inclined 30° to the left during its life on the reef. Its average growth rate is 0.35 cm/y but at the maximum

vertical angle (53°) growth rate is only 0.06 cm/y. Although interior budding is not evident in the x-radiograph of this colony, it has been observed in raised areas of this plate. Peripheral epithelial budding is dominant, however, and new corallites form in the same manner as they do on the skirts of the column and flared column morphotypes.

**GENERAL TRENDS IN MORPHOLOGY WITH DEPTH.**—*Maximum Growth Rate and Maximum Growth Angle:* Data (Figures 186, 187) from 38 colonies of *Montastrea annularis* on the maximum annual growth rate and maximum angle of corallite growth—the primary factors controlling form—indicate that the relationships with depth are probably continuous and linear. The least squares regression line in Figure 186 predicts a maximum skeletal growth rate of 0.9739 cm/y at 0 m depth and a minimum skeletal growth rate of 0 cm/y (that is, the cessation of growth) at 51 m. The regression line in Figure 187 predicts a 135.2° maximum angle of corallite growth at 0 m and a minimum angle of 0° at 50.6 m depth. The predicted maximum depth limit of about 50 m for both trends is about 10% greater than the 45 m maximum depth said to be normal for the species (Goreau and Wells, 1967).

As expected, maximum skeletal growth rate and maximum angle of corallite growth correlate positively and significantly with each other ( $r = 0.689$ ,  $p < 0.01$ ). Because the trends are covariant, morphotypes can be classified in terms of only one variable, that is, maximum angle of corallite growth:

Morphotype	Range of maximum angles (°)
Hemisphere	120–180
Tapered hemisphere	105–120
Column	75–105
Flared column	45–75
Plate	0–45

Despite the statistically significant linear depth trends, dispersion about each of the calculated lines is notable. At any given depth, specimens vary in both maximum growth rate and maximum angle of corallite growth as well as in growth form. These parameters also vary from year to year within a single colony (Figure 185).

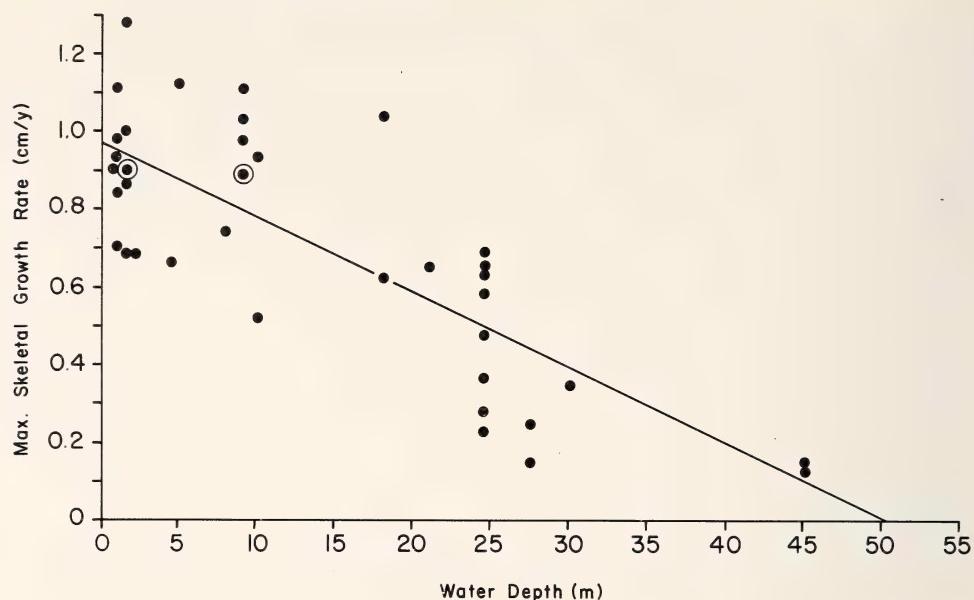


FIGURE 186.—Maximum skeletal growth rate at the crest of colonies of *Montastrea annularis* as a function of water depth, all data from Carrie Bow Cay transect except values from 45 m, Dancing Lady Reef, Jamaica (open circles with dots = duplicate values; regression equation is  $Y = -0.019X + 0.9739$ ; linear correlation coefficient,  $r = -0.729$ ,  $P < 0.01$ ).

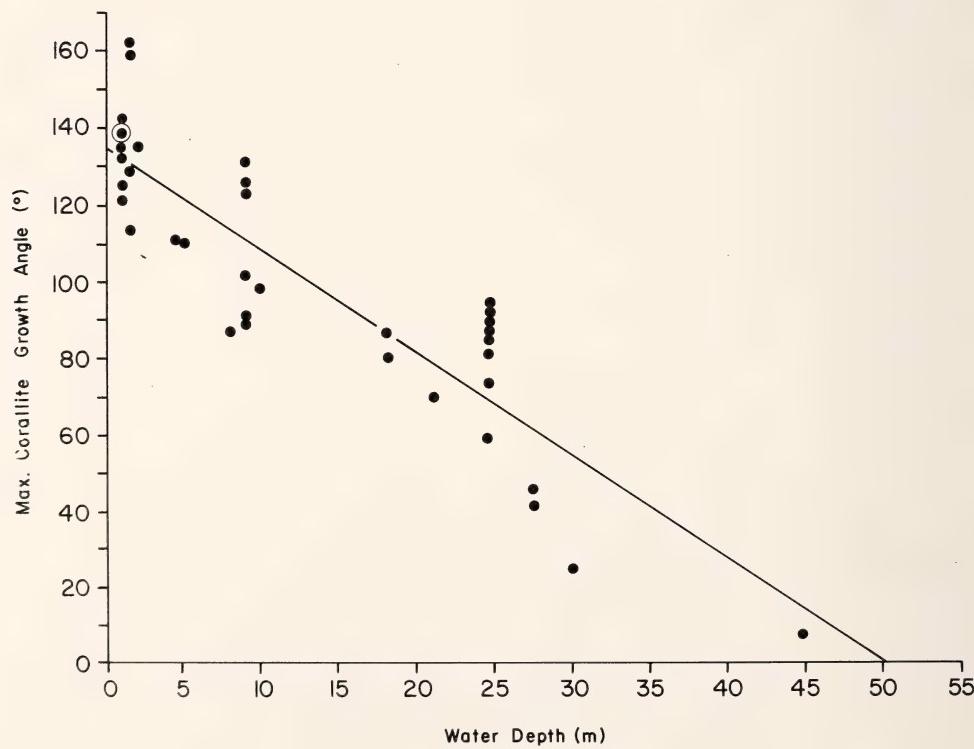


FIGURE 187.—Maximum corallite growth angle (with respect to vertical) as a function of water depth for colonies of *Montastrea annularis*, all data from Carrie Bow Cay except the 45 m value, Jamaica (regression equation is  $Y = -2.700X + 135.156$ ; linear correlation coefficient,  $r = -0.872$ ,  $P < 0.01$ ).

*Skeletal Density:* The increase in skeletal density with depth is depicted in Figure 188. The regression equation predicts a minimum skeletal density of 1.5336 g/cm<sup>3</sup> at the surface that increases to 2.0856 g/cm<sup>3</sup> at a depth of 30 m. No relationship between skeletal density and corallite growth angle could be clearly established. In some colonies, density increases from the crest to the flanks but in others it does not. Our inability to demonstrate this effect—which is readily observable in x-radiographs (Figure 185) as an increase in the ratio of dark area (high density) to light area (low density)—may be due to the comparatively large size of the skeletal slabs being considered. Slabs taken from the lower flanks of a colony generally include portions of skeleton from a previous crest. This material probably masks any differences in density between crest and flanks. If

significantly smaller slabs were used, however, measurement error due to water leakage into the skeleton would be unacceptably magnified.

*Intercorallite Spacing:* The increased intercorallite spacing at the crest with increasing depth is plotted in Figure 189. The trend in mean spacing concurs with Dustan's data (1975), although our results are not directly comparable with his because of unit differences. Our values of minimum spacing are based on single measurements for each colony; when a new interior bud is present, these values represent the distance between the new bud ( $\leq 12$  septa) and an adjacent mature corallite (24 septa). Values of maximum spacing are also based on single measurements. An interesting relationship was observed between minimum and maximum intercorallite spacing in certain colonies depending on whether a newly

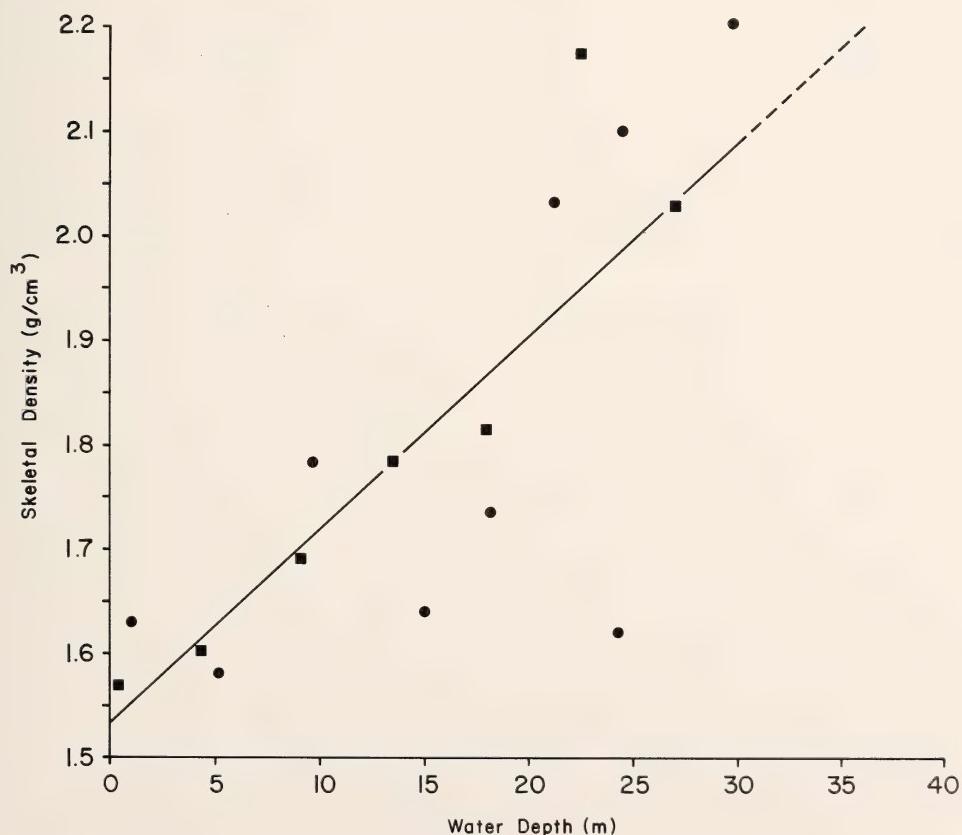


FIGURE 188.—Skeletal density as a function of water depth for colonies of *Montastrea annularis* (circles = single-value data from Carrie Bow Cay, squares = depth-specific averages from St. Croix (Baker and Weber, 1975); regression equation is  $Y = 0.0184X + 1.5336$ ; linear correlation coefficient,  $r = 0.790$ ,  $P < 0.01$ ).

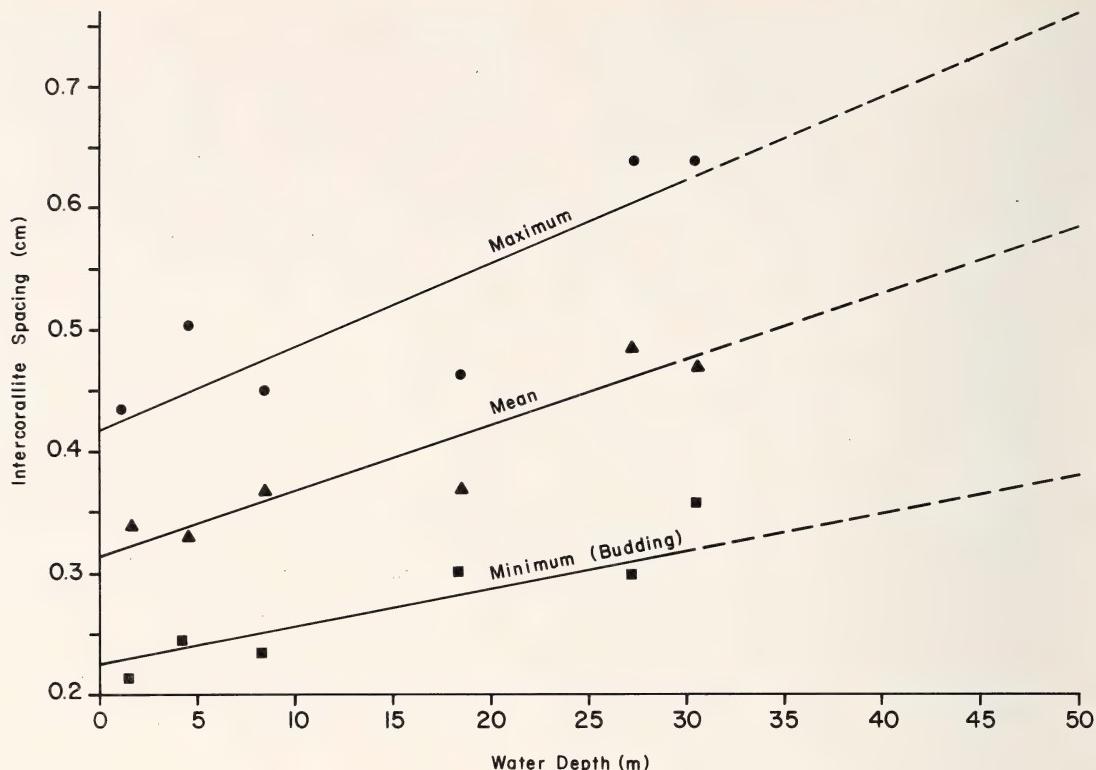


FIGURE 189.—Intercorallite spacing at the crest of *Montastrea annularis* colonies as a function of water depth; similar trends of linear equations for minimum (squares), mean (triangles), and maximum (dots) spacing suggests that interior budding is a space-controlled phenomenon (correlation coefficients: minimum,  $r = 0.950, P < 0.01$ ; mean,  $r = 0.916, P < 0.01$ ; maximum,  $r = 0.866, P < 0.05$ ).

erupted bud was present in the neighborhood of corallites. Neighborhood is taken to mean the area that encloses all nearest neighbor corallites. If a new bud was present, the distance between it and one of the mature corallites in this neighborhood would invariably be the minimum intercorallite spacing for the entire region. If a bud had not yet erupted, however, one of the distances between two mature corallites within the same neighborhood would be the maximum spacing for the region. This observation suggests that new buds originate in the largest intercorallite spaces, and that budding occurs only when sufficient space is available (that is, when the space exceeds a certain maximum distance between corallites). According to the calculated trend lines of Figure 189, this distance criterion is met when the ratio of maximum/minimum intercorallite spacing is

approximately 1.9. This ratio remains nearly constant even though both the maximum and minimum values increase significantly with depth.

The linear increase in mean intercorallite spacing with depth is mimicked by the increase in mean corallite spacing with corallite growth angle on Dustan's colony from a depth of 5 m off Jamaica. The correlation coefficient is  $r = 0.888, P < 0.01$ . The least square regression equation,  $Y = 0.00077X + 0.3136$ , predicts spacing to be a minimum of 0.31 cm at the crest and to increase to a maximum of 0.42 at 140°. Thus, intercorallite spacing varies with increasing corallite growth angle in the same way that it does with increasing depth.

TRANSPLANTATION EXPERIMENTS.—Deep-water colonies of *Montastrea annularis* transplanted to a depth of 1 m died before they could be collected.

Because the time of death could not be ascertained, these colonies were discarded. Replacements for these samples were provided by Dustan who lent us two three-year transplants from depths of 45 m to 15 m on Dancing Lady Reef, Jamaica.

All transplanted colonies surviving the experiment showed growth modifications of the type and degree expected for in situ colonies at the depths of transplantation. Figure 190 shows the changes in maximum skeletal growth rate among the transplanted specimens. Where the depth of transplantation exceeds the depth of origin, the maximum growth rate decreases, the new rate being in proportion to the new depth; where the depth of transplantation is less than the depth of origin, the maximum growth rate increases in similar fashion. The growth rates of transplanted colonies moved from 1 to 14 m are approximately the same as the growth rates of colonies moved from 45 to 15 m. Thus, the depth of origin as well

as the direction of transplantation probably have little influence on the growth rate at the transplant site. Although the growth rates of transplanted colonies are consistently below the predicted trend for in situ colonies, this result may not necessarily be significant. Colonies 1, 4, 5, and 8 have growth rates below the trend at their depth of origin, so it is not surprising to find them below it at the depth of transplantation. The maximum value of colony 3 could not be measured at the crest owing to nail damage of the polyps, which had to regenerate before normal growth could ensue (Figure 192a). Also, all colonies may have experienced a lag in growth during a period of shock immediately following the transplantation. This period of shock has been observed in other transplant experiments (Dustan, 1975) and may have contributed to the demise of our transplants from deep to shallow water. Colony 8, which was rotated (turned over) 65° and cemented at the same depth, grew at about the

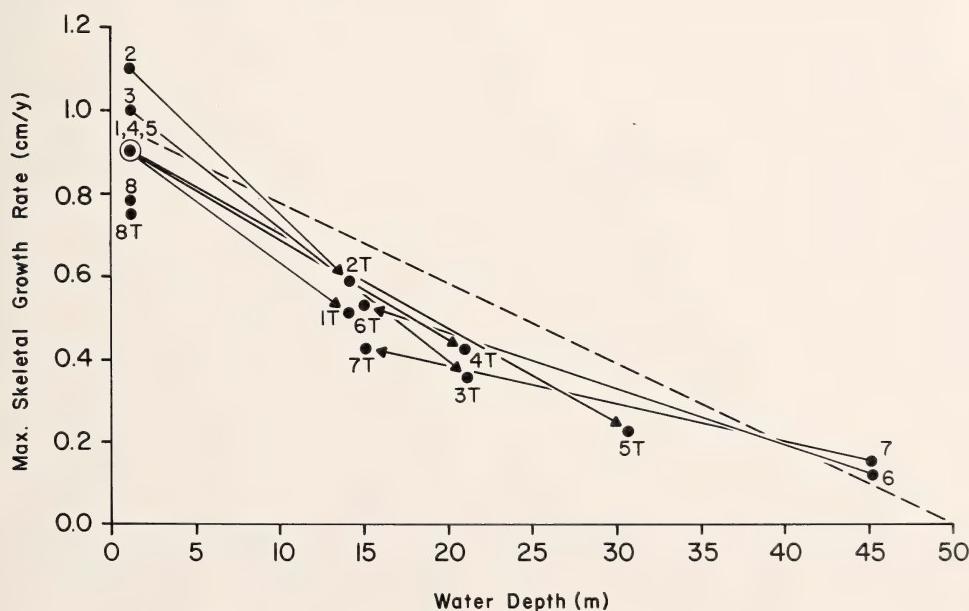


FIGURE 190.—Systematic changes in maximum skeletal growth rate at the crest for colonies of *Montastrea annularis* reciprocally transplanted for 3 years at different depths; solid lines with arrows indicate direction of transplant and change in growth rate over transplant interval; colony 8 was cemented in rotated position (65° to original orientation) at the same depth; colonies 6, 7 are from 3-year transplant data from Jamaica (courtesy P. Dustan); dashed line is the regression equation of the maximum skeletal growth rate vs. depth of in situ colonies (Figure 186).

same maximum rate at the new crest as it had at the old crest.

Changes in maximum angle of corallite growth among the transplanted corals are depicted in Figure 191. Where the depth of transplantation exceeds the depth of origin, colonies have a reduced angle of growth almost proportional to the depth of transplantation. This reduction is caused by a gradual die-back of peripheral polyps (Figure 192a). On the other hand, colonies transplanted to shallower depths show an increase in maximum corallite angle, which is caused by peripheral budding from the epitheca (Figure 192b,c). The colonies may be said to be developing flanks, and given enough time they would probably become tapered hemispheres.

The rotated colony shifted its entire annual growth pattern approximately  $65^{\circ}$  in the direc-

tion of the new vertical axis (Figure 193). New polyps appearing on the left periphery resembled those in colonies transplanted from deep to shallow water. No die-back occurred at the right periphery but the growth rate was considerably reduced.

Similar reorientation of growth pattern following rotation is evident in an accidentally overturned colony found by David L. Meyer in Panama (Figure 194). After being overturned, the crest shifted to the new vertical position, new polyp growth extended the lower left flank, and polyps on the right flank died back. Polyps on the left side of the new crest accelerated their growth whereas polyps on the right side decelerated their growth. Polyps between the old and new crest developed a sigmoid growth path after their position changed from being on the left of the old

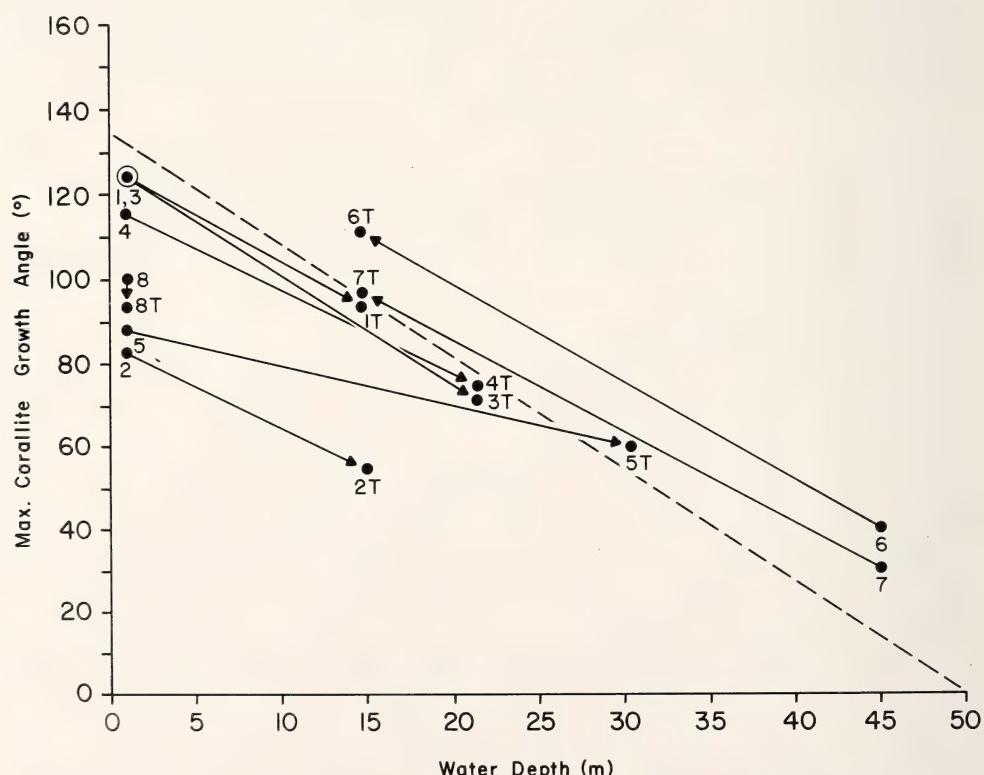


FIGURE 191.—Systematic changes in maximum corallite growth angle (with respect to vertical) for reciprocally transplanted colonies of *Montastrea annularis*; all data from Carrie Bow Cay transect except colonies 6 and 7, which were transplanted off Jamaica; for the rotated colony 8, 8T is the angle relative to the new crest; dashed line is the same regression equation for in situ colonies (Figure 187).

crest to the right of the new crest.

Transplantation-induced changes also took place in skeletal density and corallite spacing. Colonies moved to deeper water showed a significant increase in density at all growth angles (Figure 192a). Conversely, colonies transplanted to shallower water showed a marked decrease in skeletal density for all angles (Figure 192b,c).

FIGURE 192.—Growth pattern alterations in x-radiographs of *Montastrea annularis* colonies after 3 years at transplant site: a, colony 3 (Figures 190, 191), transplanted from 1 m to 20 m off Carrie Bow Cay, shows die-back of live growth surface, reduction of annual growth rate at all corallite angles, and increase in skeletal density; b and c, colonies 6 and 7 (Figures 190, 191), transplanted from 45 m to 15 m off Jamaica, show increase in maximum growth angle, increase in skeletal growth rate, decrease in skeletal density, and decrease in intercorallite spacing due to proliferation of interior buds (arrowhead = position of maximum growth angle before transplant; dot = maximum growth angle 3 years after transplant).

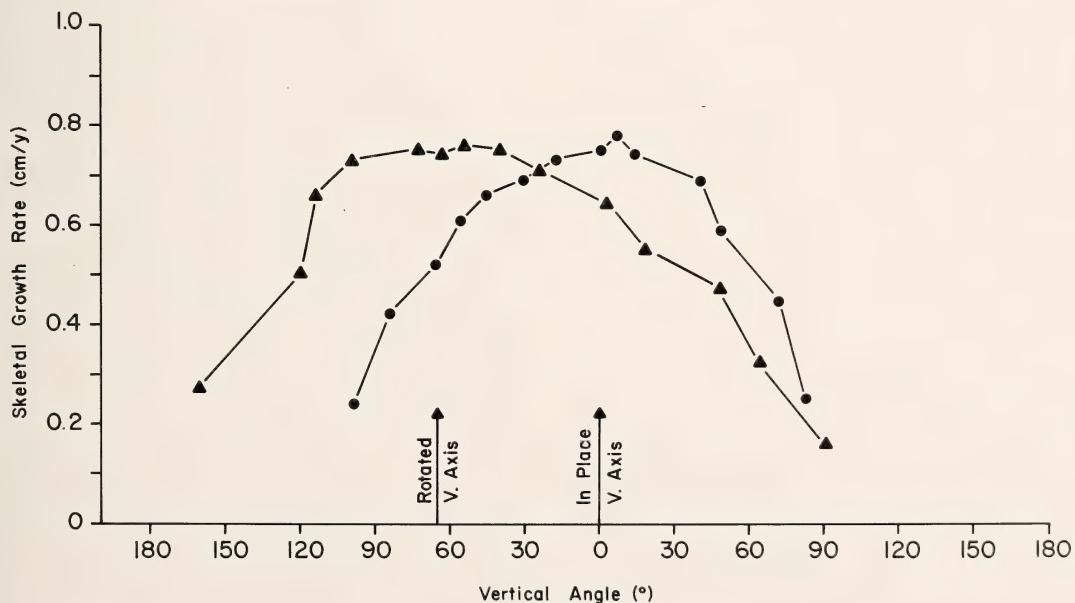
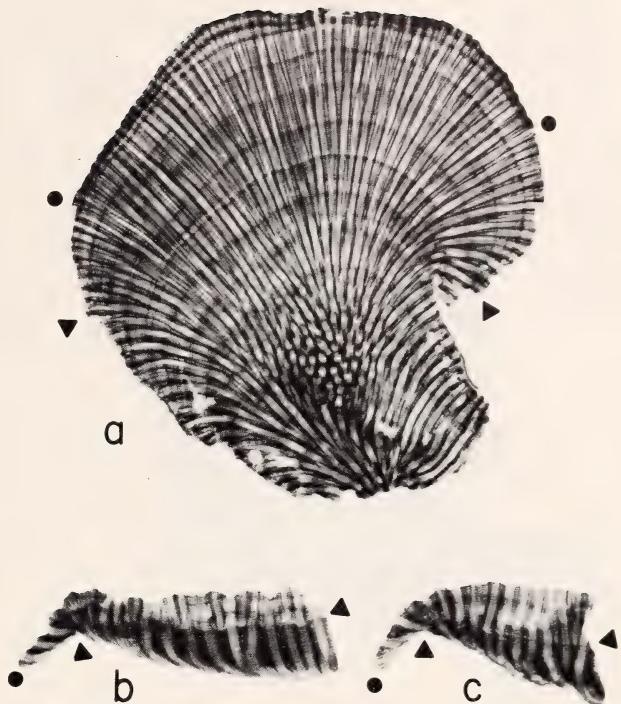


FIGURE 193.—Change in profile of average annual skeletal growth rate with respect to vertical angle for rotated colony 8 (water depth 1 m) 3 years before transplant (dot-plotted curve) and 3 years after transplant (triangle-plotted curve); after transplant, maximum skeletal growth rate remains constant, while maximum growth angle increases about 60° on left side but does not change on other side; vertical distance between curves is a measure of increase or decrease in growth rate at various locations on colony surface (vertical arrows mark positions of original and rotated vertical axes).

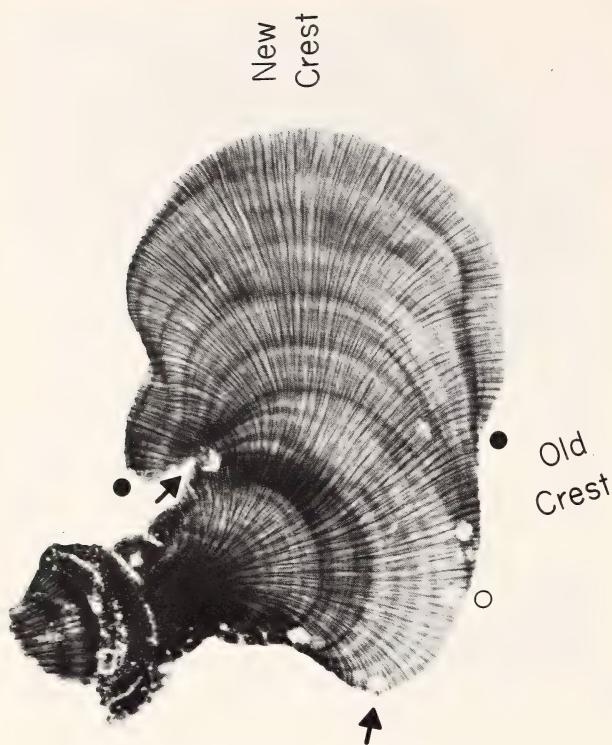


FIGURE 194.—Growth history in x-radiograph of overturned *Montastrea annularis* colony collected by David Meyer in Panama, colony oriented with living crest up; corallites between original crest and new crest develop sigmoid growth paths as they switch from left side of original crest to right side of new crest (arrow = maximum corallite growth angle before overturning; closed circle = maximum growth angle several years after overturning; open circle = intermediate die-back position of growth surface at short time after overturning).

Changes in intercorallite spacing are evident in material transplanted from deep to shallow water (Figure 192b,c), in that intercorallite spaces become filled with new buds. Because interior budding seldom occurs in the plate morphotype, the rapid proliferation of new buds appears to have been caused by altered environmental conditions at the shallower depth. Despite the decrease in spacing at the crest, spacing at the flanks—which grow at higher angles—remains greater. Changes in intercorallite spacing are difficult to observe in colonies moved from shallow to deep water (Figure 192a), but in general the corallites continue to diverge without further budding as the growth

surface expands. Budding would occur eventually, but probably at a set of wider corallite spacings.

These transplant experiments show that the morphological parameters that vary with depth and angle for in situ colonies are the same ones that undergo modification when colonies are moved between depths and allowed enough time to equilibrate with the new environment. The remarkable consistency with which transplanted colonies come to resemble in situ colonies at the same depth strongly suggests that these morphological parameters and the overall growth form are ecophenotypically controlled. Because the pattern of morphological variation closely matches the pattern of variation of submarine light distribution, the most likely factor governing this ecophenotypic response is light.

**UNDERWATER RADIANCE DISTRIBUTION.**—Data on underwater radiance used in the computer simulation program were derived from open-water measurements made at depths of 5, 10, and 20 m by Roos (1967) in Piscadera Baai, Curaçao. For each depth Roos measured two-dimensional light fields at several solar altitudes and azimuths. He mathematically corrected the azimuthal data to the solar plane, and averaged these values in order to obtain an integrated light distribution. His final data (Roos, 1967, table 11)—converted from microamperes to footcandles using his laboratory to field instrument calibration ratio of 12.5 lx/ $\mu$ A and the standard International System ratio of 10.8 lx/fc—allowed us to compute least squares regression lines of the logarithms of his specific angular radiances ( $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ ,  $90^\circ$ ,  $120^\circ$ ) with increasing depth in order to obtain five equations that could be used to calculate angle-specific radiance for any depth. Solution of the equations at five-meter intervals down to 45 m gave us a set of gridded data from which the contour map in Figure 195 was manually generated. Considering the angular limits of the original data, contours at angles greater than  $120^\circ$  are based on extrapolations and should be interpreted with caution. However, because this portion of the contour map is seldom used in our simulation program, it has not been problematic.

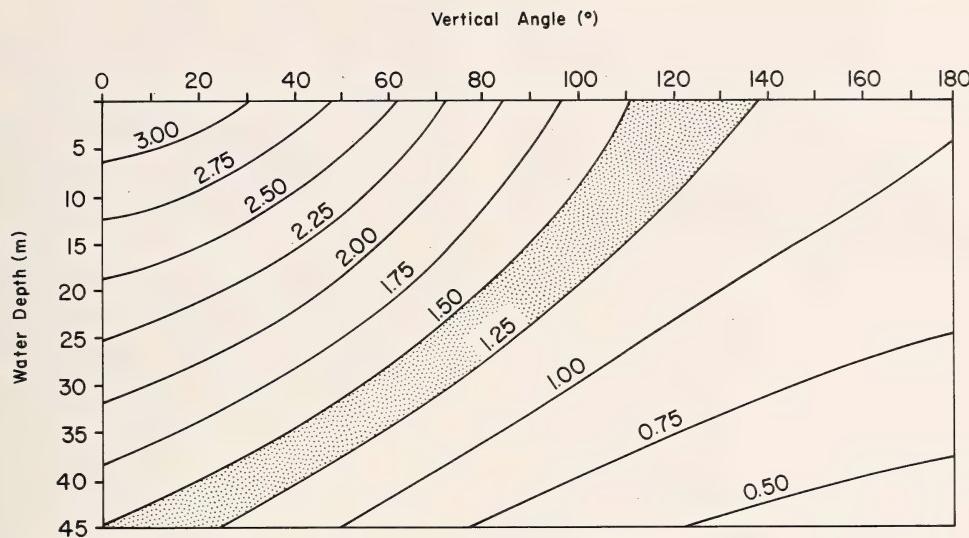


FIGURE 195.—Logarithm (base 10) of radiance in footcandles contoured with respect to water depth and angle from the vertical, radiance data derived from Roos (1967, table 11). The dotted area is the range of vertical radiance between 45 m, the reported maximum depth of occurrence, and 50 m, the predicted maximum depth of occurrence of *Montastrea annularis* (Figures 186, 187). In this depth range, the maximum growth angle is close to 0°. At shallower depths the same radiance exists at greater vertical angles, where it defines the maximum corallite growth angle.

**LIGHT-RESPONSE MODELS FOR CALCIFICATION.**—*Model 1:* The light-response model for calcification in our previous simulation of skeletal growth of *Montastrea annularis* (Graus and Macintyre, 1976; Graus, 1977) was based on the light and carbon dioxide curve reported by Barnes and Taylor (1973). This earlier model (Model 1) assumed that the rates of algal symbiont photosynthesis and skeletal calcification were linearly related and therefore would have similar mathematical expressions with respect to light intensity. A subsequent experiment by Chalker and Taylor (1975) supported this assumption in observing that the rate of calcification in *Acropora palmata* increases proportionately with subsaturating light intensity up to 10,500 lx. This result, according to the authors, "agrees with studies of photosynthetic carbon fixation in hermatypic corals" (p. 328). Despite this qualitative agreement, however, the quantitative relationship between the rate of photosynthesis and the rate of calcification still remains uncertain.

In our model, the Barnes and Taylor (1973)

curve was fitted with the exponential function

$$r = R[1 - e^{-k(I-I_c)}]$$

using the reduced major axis method (Imbrie, 1956). This function states basically that skeletal growth rate,  $r$ , depends on variation in light intensity,  $I$ . The relationship is regulated by three constants:  $R$ , the maximum skeletal growth rate at saturation light intensity;  $I_c$ , the light intensity below which no long-term growth occurs; and  $k$ , a constant that is equal to the slope of the linearly transformed equation. In the equation,  $R$  is set at 1.1 cm/y, which is equivalent to the maximum skeletal growth rate of any Belizean colony (pre-1975 collection). This rate was measured at the crest of a hemispherical colony collected from a depth of 1 m. The value of  $I_c$  was set at 29 footcandles (1 fc = 10.8 lx = 1.6  $\mu$ W/cm<sup>2</sup>) which corresponds to the vertical radiance at 45 m (extrapolated from light data of Roos, 1967). This depth is considered to be the normal maximum depth of the species (Goreau and Wells, 1967) and is close to the maximum depth for *Montastrea*

*annularis* in Belize. Because of the pattern of underwater light distribution,  $I_c$  not only controls the maximum depth of the species, but also the maximum angle of corallite growth. Use of this equation permitted functional expression of the Barnes and Taylor (1973) curve; however, other fitting equations such as a polynomial, Michaelis-Mention equation (WetHEY and Porter, 1976) could have served as well.

Model 1 assumed that a single light-response curve governs calcification for the entire species. Recent reports suggest that the zooxanthella, *Gymnodinium microadriaticum* Freudenthal has high-light and low-light ecotypes that inhabit, respectively, shallow and deep populations of reef corals (Barnes and Taylor, 1973; Dustan, 1975; WetHEY and Porter, 1976). If the photosynthetic response mechanism of these ecotypes is indeed distinct, there may also be different light-mediated calcification curves; however, any calcification differences between shallow and deep-water populations have yet to be demonstrated experimentally.

Model 1 also assumed that skeletal growth rate in cm/y is proportional to calcification rate in g/cm<sup>2</sup>/y. This assumption is correct if the average density of the skeleton is constant. Information about systematic density variations was not available before 1975, but since that time various workers (Baker and Weber, 1975; Dustan, 1975; Highsmith, 1979; and this paper) have shown that average skeletal density increases proportionately with depth and probably with corallite growth angle and therefore is apparently dependent on light intensity.

*Model 2:* Although light-mediated photosynthesis and calcification are known to be related (Vandermeulen et al., 1972), the biological mechanism and the mathematics of the interaction are still conjectural. Because acceptance of Model 1 depends on the outcome of this continuing discussion, we decided to propose an independent empirical model for calcification in relation to light (hereafter referred to as Model 2; see Appendix for summary of computer program) based on our skeletal measurements of in situ colonies of *Montastrea annularis* from Carrie Bow Cay. In

restructuring the original model, we added new information on the relationships between light and skeletal density and intercorallite spacing.

Calcification rate in Model 2 is calculated by the method of Baker and Weber (1975) as follows:

$$\text{Calcification rate (g/cm}^2/\text{y}) = \text{skeletal density (g/cm}^3) \times \text{skeletal growth rate (cm/y)} \quad (1)$$

From the regression equations shown in Figures 188 and 186, skeletal density and skeletal growth rate can be expressed as a function of depth:

$$\begin{aligned} \text{Skeletal density} &= 0.0184 \times \text{depth} \\ &+ 1.5336 \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Skeletal growth rate} &= -0.0191 \times \text{depth} \\ &+ 0.9739 \end{aligned} \quad (3)$$

A least squares regression of the logarithm (Ln) of mean vertical radiance with depth in Curaçao (Roos, 1967, table 11) gives the following linear equation:

$$\text{Depth} = \frac{7.4696 - \text{Ln (Radiance)}}{0.08881} \quad (4)$$

Sequential substitution of the equations (4) → (3), (2) → (1) yields calcification rate in terms of light intensity. This relationship, plotted in Figure 196, shows how average calcification rate at the crest of the colony declines with attenuation of vertical radiance.

Although this model is derived from morphological measurements, use of it does not predetermine the growth form of a simulated colony. It merely establishes the skeletal growth rate at the crest of a colony at any given depth. Growth rates for corallites in other orientations, and hence the growth form of the colony, depend upon the radiance distribution at the prescribed depth.

Figure 197 shows that the light-response curves for Model 1 and Model 2 are similar in overall shape but differ in detail. Both the maximum growth rate and the minimum light intensity for growth are greater for Model 1 than for Model 2.

**SIMULATION EXPERIMENTS.—Morphotypic Variation with Water Depth:** Model 2 simulations of colony growth of *Montastrea annularis* from depths

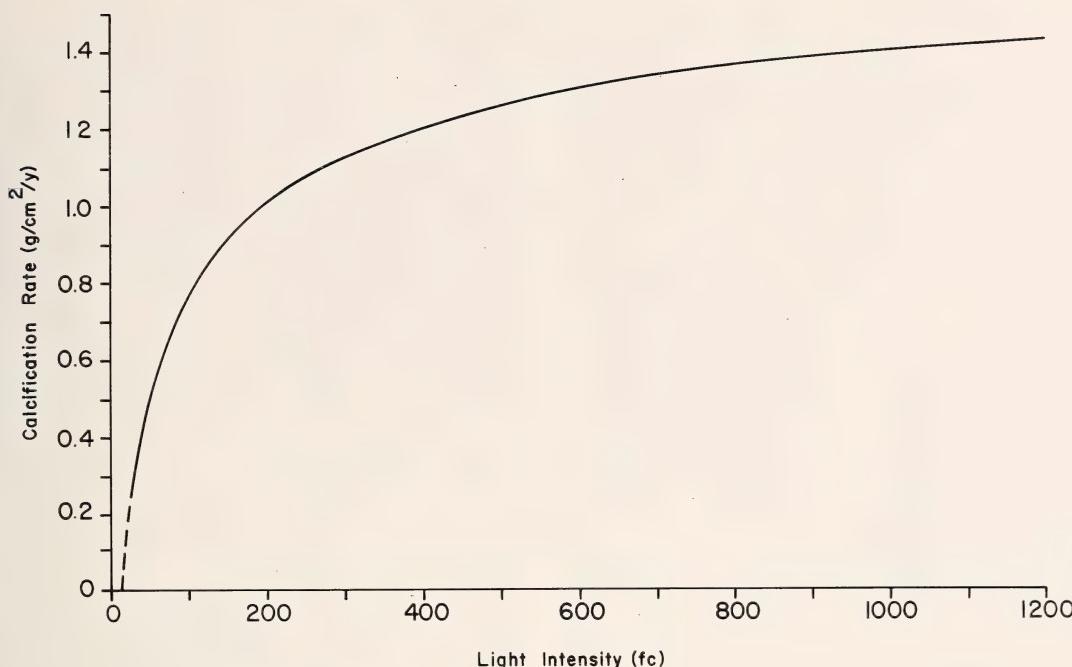


FIGURE 196.—Calcification rate for *Montastrea annularis* as a function of light intensity used in Model 2 computer simulations; curve derived from liner equations fit to empirical mesurements of maximum skeletal growth rate, skeletal density, and light in relation to depth (Figures 186, 188).

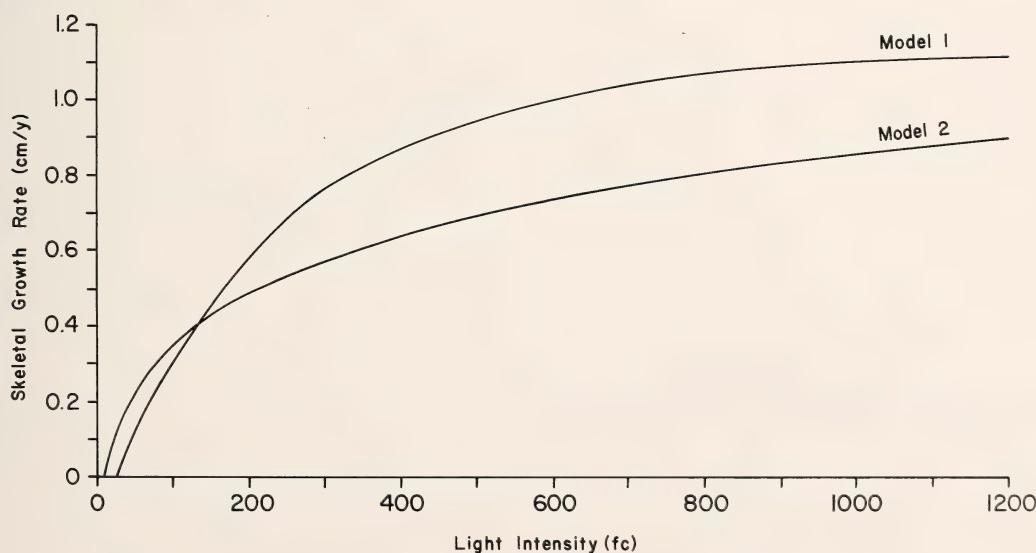


FIGURE 197.—Comparison of Model 1 and Model 2 skeletal growth rate curves in relation to light intensity. Minimum light intensity of long-term growth for 1 is 29 footcandles; for 2 it is 19 fc. Maximum growth rate asymptote for 1 is 1.1 cm/y; for 2 it is 0.9739 cm/y. Curves intersect where light intensity is 135 fc and skeletal growth rate is 0.4 cm/y. Vertical distance between curves is the difference in skeletal growth rate at that light intensity.

of 1 m to 40 m appear in Figure 198. These simulations depict the annual growth bands, corallite growth paths, and the development of corallum geometry as seen from x-radiographs of vertical skeletal slabs (compare with Figure 185). Although these are distinct stages, the program can produce any number of transition forms, which, taken together, approximate a continuous distribution. Some input and output values for these simulations are given in Table 35.

Growth rate values at the crest (Table 35, column 3) are derived from the linear equation in Figure 186. Growth rates away from the crest, as well as the maximum corallite growth angles, depend entirely on the angle-specific radiance values and their conversion to growth rates via the parametric equations of Model 2. The maximum growth angles in the simulations (Table 35, column 4) are the angles for which the corallite growth rate is 0.1 cm/y. These angles correspond closely to values predicted by the regression equation (Figure 187) for real colonies growing at the same depths. This outcome lends independent support for Model 2.

The sequence of simulations in Figure 198 compares favorably with the sequence of real colonies in Figure 185. The whole set of morphotypes is represented in correct order, and the growth details are also similar. As in the real colonies, the maximum growth rate for the simulated colonies occurs at the crest, and the rate

diminishes gradually with increasing angle to a minimum of 0.1 cm/y. In the hemispheric colonies (Figure 198a-c) the corallites near the crest follow linear paths. Farther from the crest, where differential growth of the surface is greater, the corallites curve away from the crest. In the column morphotype (Figure 198d) corallite curvature begins in the crest region. Colonies a-d begin from a circular base of the same radius, but only in d does the colony become a column.

Colonies e-g are developing skirts and plates because the annual growth rate of the surface has fallen below 10%. As in real colonies, the skirts and plates develop a concave upward form because each new peripheral bud grows at a lower angle than its predecessor. Plate g has become completely horizontal.

Printout records show that the rate of increase in surface area diminishes annually. This means that once the rate falls below 10%, it will continue to force, at an ever increasing rate, the growth of the skirt or plate. Even the hemispheric corals will, in time, develop skirts and plates. We estimate that this should happen after about 25–30 years of growth. This conclusion agrees with the observation that large hemispherical colonies of *Montastrea annularis* in shallow water frequently develop skirts on their lower flanks.

The simulated colony of Figure 198g evidently compares morphologically with the real colony of Figure 185e, but their depths of occurrence do not agree. This difference can be accounted for if one remembers that the real plate had an in situ inclination of 30°. Thus, although the real specimen has a platelike form, it is probably just an isolated flank of a flared column.

*Model 1 and Model 2 Morphotypes Compared:* Results of Model 1 and Model 2 simulations can be compared from output in Figure 198 and output in Graus and Macintyre (1976, fig. 1). The light vs. skeletal growth rate curves in Figure 197 also show the expected outcome. Whenever light intensity exceeds 135 fc (the intersection point of the two curves), skeletal growth rate is greater for Model 1; conversely, whenever it falls below 135 fc the rate is greater for Model 2. According to

TABLE 35.—Input and output values for Model 2 simulation of *Montastrea annularis* growth; in each run, PGRATE is 10% (see Appendix); radiance distributions based on open-water data (see Figure 195) with no reflection added

Water depth (m)	Growth interval (y)	Base radius (cm)	Growth rate at crest (cm/y)	Maximum growth angle (°)
1	15	2.0	0.959	117
5	15	2.0	0.869	114
10	15	2.0	0.795	97
20	25	2.0	0.587	82
30	10	5.0	0.408	61
35	15	8.0	0.304	45
40	20	8.0	0.204	24

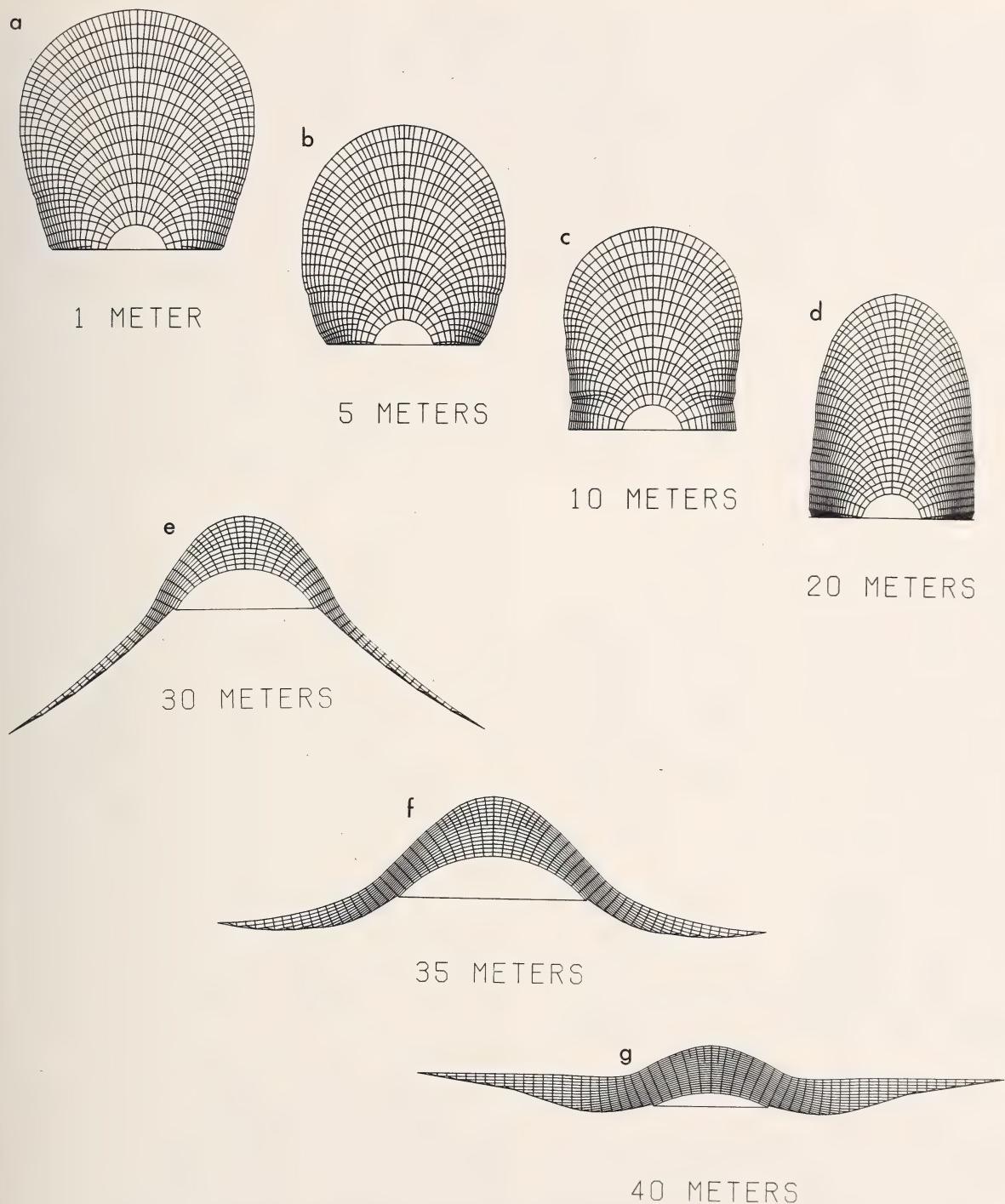


FIGURE 198.—Computer simulation plots of the growth of *Montastrea annularis* colonies in relation to submarine radiance distribution from depths of 1 m to 40 m, generally reproducing the depth-related morphotypic gradient shown in Figure 185; simulations utilize the calcification-light relationship of Model 2 in Figure 196 and open-water radiance data from Roos (1967, table 11) contoured in Figure 195.

Figure 195, vertical radiance of 135 fc ( $\log_{10} 135 = 2.13$ ) occurs at a depth of 27 m on the reef. Above this depth, then, the growth rate at the crest is greater and declines faster with corallite growth angle for Model 1 colonies than for Model 2 colonies. Model 1 colonies are thus relatively more peaked than Model 2 colonies. Below 27 m the reverse is true. Because the minimum threshold light intensity is lower for Model 2 than for Model 1, Model 2 colonies always have a greater maximum growth angle at any depth than Model 1 colonies. Therefore the transition depths between morphotypes as well as the maximum growing depth are greater for Model 2 colonies than for Model 1 colonies. Despite measurable differences in the morphotypes produced by the two models, the differences are not readily discernible in the graphical outputs. Hemispheres from the two models are similar and can be distinguished only by careful observation.

The simulation results of Model 1 and Model 2 were compared in order to examine the morphological effects that would result if *Montastrea annularis* had shallow- and deep-water populations with separate light-calcification curves. Such a situation exists in the light-productivity curves of shallow- and deep-water populations, respectively, of *Pavona praetorta* Dana (WetHEY and Porter, 1976). These curves closely resemble the light-calcification curves of Model 1 and Model 2. If (1) the light-calcification differences of these populations of *M. annularis* are no greater than the differences between the light-productivity curves of WetHEY and Porter (1976) and (2) these populations are separated by depth, except for a narrow overlap zone between 15 m and 20 m, as suggested by Baker and Weber (1975) and DusTAN (1979), then the shallow population would have only hemisphere and tapered hemisphere morphotypes, whereas the deep population would have only the flared column and plate morphotypes. In the overlap zone, the column morphotype could predominate for both populations. According to the simulation models, these column morphotypes of the two populations would be distinguished by the range of maximum corallite growth angle:  $82^\circ$  to  $92^\circ$  for the shallow popu-

lation,  $98^\circ$  to  $108^\circ$  for the deep population. However, because the ranges are close and because other factors such as slope, bottom reflection, and shading by neighboring organisms also influence the maximum angle, recognizing the two populations in the overlap zone would be difficult. Therefore shallow and deep populations cannot be distinguished with certainty on the basis of growth form. Furthermore, the simulation models suggest that the sequence of morphotypes is a single continuous gradient with depth.

*Morphological Effects of the Bottom Reflection:* In Model 1 simulations, a 5% light reflection was added to all radiance values to render the open-water data of Roos (1967, table 11) more realistic in terms of benthic lighting conditions. For Model 2 simulations, this procedure was eliminated routinely because we could not accurately express the distribution of reflection to all radiance angles. However, because corals grow on a highly reflective substrate, it is important to speculate on the possible morphological effects of reflection. Figure 199 shows the effect of including different reflection values in Model 2. As can be seen, with increasing percentage reflections there is a progressive increase in the growth of the lower flanks with respect to growth at the crest. Even with 2.5% reflection, the maximum angle of corallite growth extends to  $180^\circ$ . Thus, if a colony were somehow suspended above the substratum it could grow vertically downward. Other differences not apparent in the diagrams are the decrease in skeletal density and the increase in corallite spacing at all corallite growth angles.

Reflection from the bottom substrate plays a significant role in the morphology of the colonies but the amount of reflection is difficult to establish. Brakel (1979) found an average of 18% bottom reflection for sandy substrates and 5% for living substrates, but these values can vary considerably from one microhabitat to another.

The morphological effects of reflection are probably greater for shallow-water colonies than for deep-water colonies. If we consider two colonies, one shallow and one deep exposed to the same percentage reflection (for example, 5% of penetrating light), the amount of additional re-

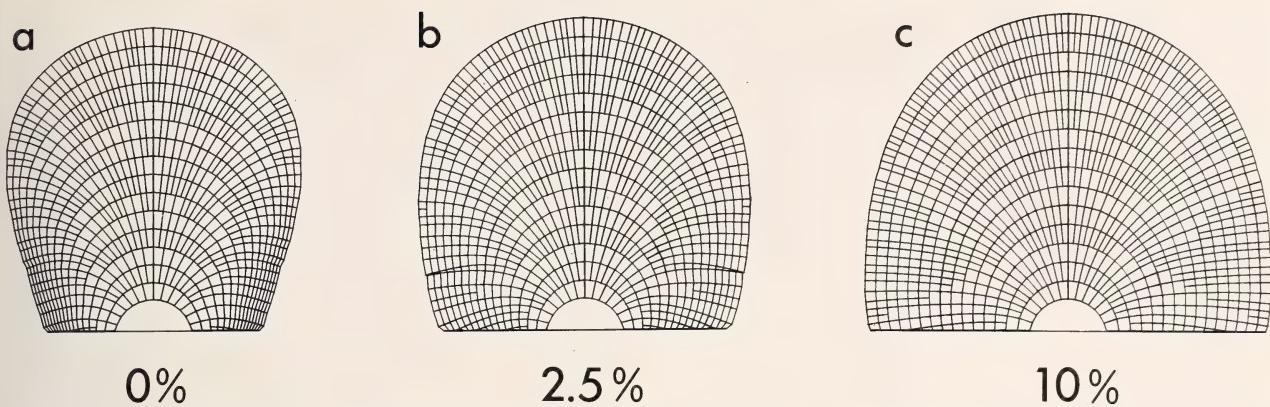


FIGURE 199.—Simulations of morphological effects on colony at 1 m depth resulting from the addition of increasing amounts of light reflection (from bottom substrate) to open water radiance data: *a*, no addition; *b*, plus 2.5%; *c*, plus 10%. Growth increments that include reflection are obtained by adding the percent of vertical radiance equally to radiance values at all vertical angles.

flected light in shallow water would be greater than that in deep water. Therefore, this factor and the postulated relationship of corallite growth rate to absolute rather than relative radiance suggest the morphological effects of reflection should diminish toward deep water. Thus, any additional reflection would make shallow-water colonies more rounded and increase the transition depths between the morphotypes but it should have relatively little effect on deeper water colonies.

*Transplantation of Colonies:* Figure 200 shows the simulation of transplanted colonies from shallow water to deep water. The transplant conditions (from 1 to 20 m) in Figure 200*a*, left, are comparable to those of the real colony in Figure 192*a*, and the outcome is nearly the same (Table 36).

As in the real colony, there is reduction of maximum growth angle, which involves a die-back of the live surface, the skeletal density increases at all corallite angles, and the intercorallite spacing becomes wider as the corallites diverge without producing interior buds. Figure 200*a*, right, shows an extension of the experiment to 9 years at the transplant site. The transplanted colony has grown a skirt. Although skirt development on a real transplanted colony has not been observed, we would expect it to occur in a natural experiment of this duration. Figure 200*b*

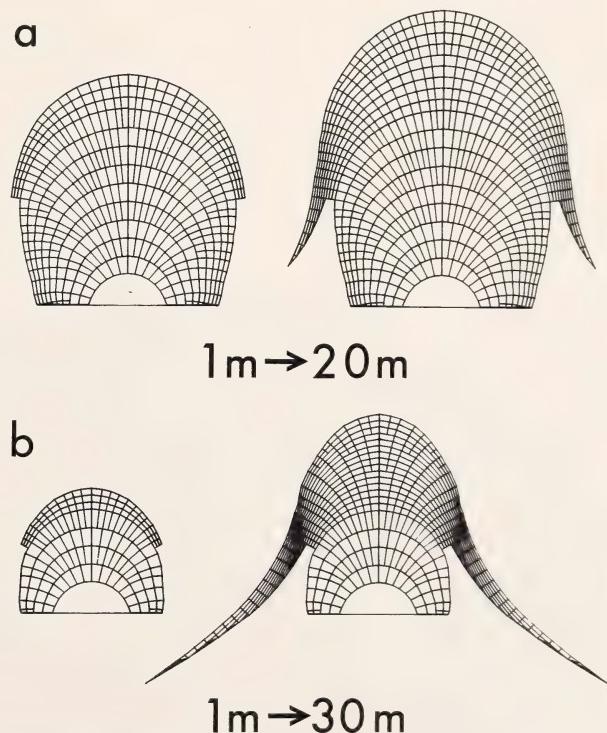


FIGURE 200.—Simulations based on Model 2 showing 3 years (left) and 9 years (right) of growth in shallow to deep water transplant experiments: *a*, transplanted from 1 m to 20 m; *b*, from 1 m to 30 m. As in actual transplant experiments, simulated transplanted colonies experience reductions in growth rate and maximum corallite growth angle proportional to transplant depth, and increases in skeletal density and intercorallite spacing. After 3 years at transplant depth, simulated colonies begin to develop skirts (not observed in actual colonies.)

TABLE 36.—Comparison between growth data at different depths for real and simulated *Montastrea annularis* transplanted colonies; both transplants from 1 m to 20 m lasting for three years

Specimen	Maximum growth rate (cm/y)		Maximum growth angle (°)	
	1 m	20 m	1 m	20 m
Real colony 3 (Figure 192a)	1.000	0.390	125	78
Simulated colony (Figure 200a left)	0.959	0.587	117	82

shows the same type of simulation experiment for a 1 m to 30 m transplanted colony. Comparison of the simulation output (Table 35) with those of the real colony 5 (Figures 190, 191) again shows a close similarity of results.

Similar simulated transplant experiments from deep water to shallow water were not attempted because the computer program would have to be modified. We have no doubt they could be done successfully. In addition, it should be possible to simulate the change in growth pattern produced by experimental or natural rotation of the colony (see Figure 194). For this, the program would have to be altered so that it calculates both sides of the colony (at present, because only one half of the colony is calculated, it must be bilaterally symmetrical).

### Conclusions

Stained colonies of *Montastrea annularis* and their x-rays have provided a detailed understanding of the major geometric parameters that dictate the growth and morphotypic variations of this species. In all colonies studied, for example, maximum skeletal growth rate occurs in vertically oriented corallites that are usually situated at the crest of the colony and the rate of growth diminishes systematically with corallite growth angle. The maximum growth rate and the maximum vertical angle of corallite growth also diminish linearly with depth. These varying combinations of parameters produce a continuous spectrum of

corallum growth forms from the surface to 50 m, ranging from hemispheres, through tapered hemispheres, columns, and flared columns, to plates. Similarly, skeletal density and intercorallite spacing gradually increase with increasing corallite angle and depth of colony growth.

Transplanted colonies in both Belize and Jamaica undergo nearly complete modification of all the described parameters, and after three years the growth form closely matches that of in situ colonies at the same depths. These results demonstrate that morphotypic variation of *Montastrea annularis* with depth is predominantly an ecologically rather than a genetically controlled phenomenon. A similar conclusion was reached by Foster (1979), who found, using similar transplant experiments, a high degree of phenotypic plasticity in the corallite microarchitecture of this species.

With these new data we were able to construct a computer simulation model to evaluate the relationship between submarine light distribution and the growth forms of *Montastrea annularis*. Unlike our earlier model (Model 1 in Graus and Macintyre, 1976), which was based on experimental studies of photosynthesis and calcification in response to light intensity, this empirical model (Model 2) was based on calcification in relation to light as established by our measurements of skeletal characteristics relative to corallite orientation and water depth.

Simulation experiments with Model 2 show that as in the case of Model 1 a broad range of morphotypes produced are comparable to the corallum growth form sequence observed with increasing depth on the Carrie Bow reef transect. In addition, simulations of the transplant experiments replicate the observed changes in growth forms and show that the modifications result from a combination of altered skeletal growth rate, maximum corallite growth angle, skeletal density, and intercorallite spacing. Simulation experiments on the effects of bottom reflection indicate that variation of the lighting conditions in the microhabitat can significantly alter corallum morphology.

Our light-response model was developed to test quantitatively a working hypothesis, the details of which are constantly being revised as new data are obtained on the skeletal development of tropical reef corals. In producing morphological variations comparable to those in colonies from habitats of known light fields, this model confirms that light is the major factor controlling the skeletal morphogenesis of *Montastrea annularis*. Many other factors not specifically considered by this model also influence the skeletal development of *M. annularis*, such as the symbiotic growth interaction of this coral and the sponge *Mycale laevis* (Goreau and Hartman, 1966).

It should also be noted that ambient light conditions can vary considerably within habitats at the same depth. For example, shallow-water corals growing in shaded microhabitats or on sloping substrates exhibit skeletal (morphogenesis) characteristics normally associated with colonies in deeper water. Such variations in light field and related variations in skeletal characteristics must be taken into account whenever our findings are used to interpret paleoenvironments.

That is to say, dense platy growths of *M. annularis* might indicate either deep water or restricted light conditions in a shallow environment. On the other hand, porous hemispherical growths would clearly indicate a shallow-water habitat. A relatively porous columnar colony might also be used to establish intermediate paleodepths in the range of 15–25 m; however, crowding of colonial development or bioerosion on the colonial flanks can produce pseudo-columns in very shallow water.

In restricting our field observations to relatively small, isolated, smooth-shaped colonies, we have not taken into account variations in shape and colonial architecture of other *Montastrea annularis* colonies within the same reef habitat. For example, in the shallow back-reef area off Ambergris Cay (Figure 201a), one massive development of smooth-surfaced "knobby" (terminology in Dus-tan, 1975) *M. annularis* has some areas of distinctly "lumpy" surfaces. Although these two surface types have a similar yellow-brown color, the "lumpy" areas have denser skeletons, wider corallite spacings, and greater corallite relief than the "knobby" growths. In the same back-reef

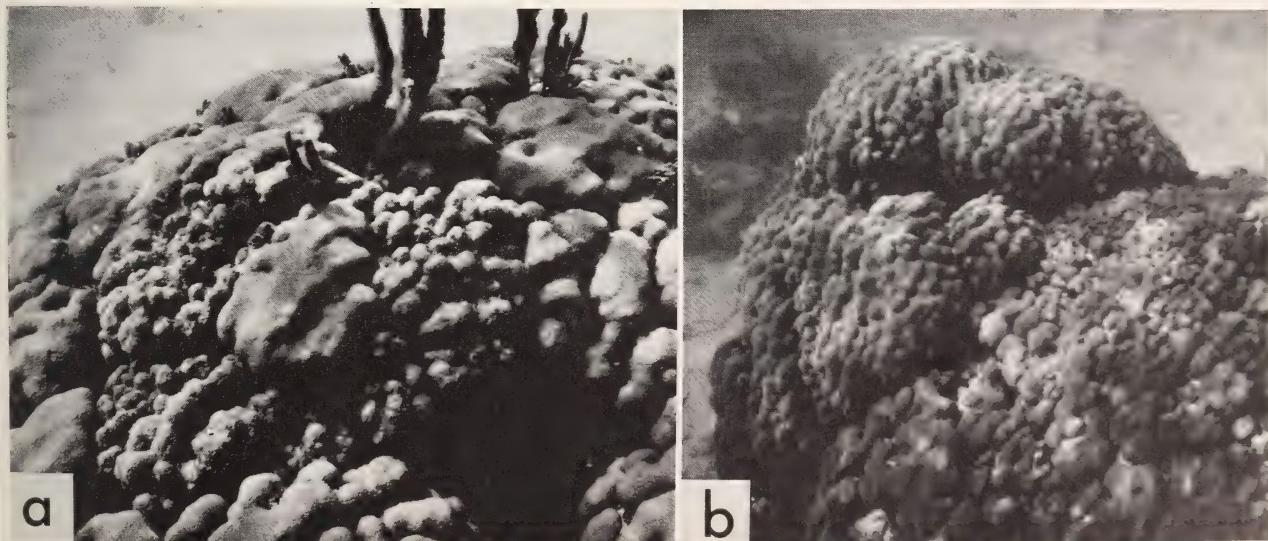


FIGURE 201.—Variations in colonial growth of *Montastrea annularis* in patch reefs in the shallow back-reef area off Ambergris Cay: a, large yellow-brown development of *M. annularis* with areas of "lumpy" widely spaced corallites between relatively smooth-surface "knobby" growth; b, yellow-brown isolated "knobby" *M. annularis* in the foreground, which contrasts sharply with continuous dark brown surfaces of "lumpy" growth in background.

area, dark brown, "lumpy" *M. annularis* can be found growing in juxtaposition with yellow-brown "knobby" colonies (Figure 201b). In the latter case, the colors of the various growth forms differ, although the skeletal density and corallite surface characteristics are similar.

These variations in skeletal morphogenesis—

which have been observed in the deeper fore-reef as well as the shallow back-reef areas off Carrie Bow Cay—are still unexplained. The lack of evidence that this skeletal development is a response to ecological conditions suggests that it could be genetically determined.

## Appendix

### SYNOPSIS OF MODEL 2 COMPUTER PROGRAM

The computer program for simulation of growth of *Montastrea annularis* is stored at Museum of Natural History, Smithsonian Institution, and is available by contacting the authors. The program written in FORTRAN IV is divided into two parts: a main program, which performs the substantive calculations, and a plotting program, which generates plotted output on a Calcomp (California Computer Products) plotter. The main program consists of seven routines, which are described below in program order.

#### 1. READ INPUT VARIABLES

External communication with the program is carried out by entering values of the following six variables, which establish the experimental conditions for each simulation run:

NYEARS numbers of years of growth of simulated colony

RADNCE sequence of depth-specific radiance values at 5° intervals from 0° (up) to 180° (down)

REFL percent of vertical radiance from bottom substrate to be added to all radiance values

PGRATE minimum allowable annual increase in colony surface area

RBASE radius of circular base of simulated colony

TPLANT transplant switch that tells the program to grow the colony using two

different sets of radiance data, one at the origin depth and one at the transplant depth

#### 2. CALCULATE ANGLE-SPECIFIC ANNUAL GROWTH INCREMENTS

The 5° RADNCE values are first linearly interpolated to obtain values at 1° intervals, and the entire radiance distribution is then smoothed using the three point moving average method. The light values for all angles are then converted into annual growth increments by the sequence of parametric equations of Model 2. The maximum growth angle is set at the angle for which the annual growth increment equals 0.1 cm/y. This corresponds with the observation that if a polyp survives a year, it will grow at least at that rate.

#### 3. ESTABLISH COLONY BASE AND INITIAL CORALLITE POSITIONS

The simulated colony starts growing on a circular base of radius, RBASE. Although a circle adequately approximates the shape of an early growth stage of a colony, the program can be easily modified to accept basal coordinates from a real specimen. The base is positioned so that its center is on the Y-axis at or near origin of the rectangular coordinate system. The Y-axis is also the vertical symmetry axis of the colony. The negative Y-quadrant is not displayed; thus, the X-axis is the flat bottom substrate.

The terminus of the first corallite is placed at the intersection of the circular base with the  $Y$ -axis, and is assigned a corallite growth angle of  $0^\circ$ , thereby establishing its orientation perpendicular to the base. The location of the second corallite is then placed on the perimeter in the positive  $X, Y$  quadrant, 1.5 times the minimum budding distance (IPDIST) from the first corallite. Its corallite growth angle, also perpendicular to the base, is the angle between vertical and a radius drawn from the center of the circle to the coordinates of the second corallite. Additional corallites are positioned in the same manner, relative to the previous corallite, until the maximum growth angle is reached.

#### 4. CALCULATE NEW GROWTH SURFACE AND CORALLITE POSITIONS

The colony grows beyond the base in yearly or other regular events up to the number specified by NYEARS. Corallite growth angles are first converted into annual growth patterns by adding the various calculated annual growth increments to the terminal positions of the corallites in the directions specified by the growth angles. These projected coordinates define the next annual growth surface of the colony.

The corallites cannot be extended merely to the new surface, however, because most of them would violate the rule that they grow perpendicular to that surface. To solve this problem, the correct path of a corallite to the new growth surface is determined by calculating a perpendicular line from the previous corallite position to a line segment extending between the projected coordinates of flanking corallites. The growth increment is then adjusted to correspond with the new growth angle.

#### 5. CALCULATE COLONY SURFACE AREA

In computing the live surface area, the colony is assumed to be a radially symmetric solid of revolution with a vertical axis of symmetry. Horizontal sections cut through the colony connecting the coordinates of the corallites divide the colony into a series of trapezoidal solids. The sum of the external surface areas of these trapezoidal

segments is the total living surface area of the colony. The area of the new growth surface is calculated and then compared with the area of the previous growth surface. If the increase exceeds the minimum growth rate specified by PGRATE, program control transfers to the interior budding routine; if not, the program control transfers to the peripheral budding routine below.

#### 6. PERIPHERAL BUDDING

Peripheral budding occurs only when the annual increase in surface area falls below the minimum value specified by PGRATE. In this routine, a new bud is added at a distance  $1.5 \times$  IPDIST from, and at a growth angle  $3^\circ$  less than, that of the terminal corallite. The growth angle of the new bud is prevented from becoming less than  $0^\circ$ . After addition of the new bud, the total surface area is recomputed and compared with the area of the previous growth surface. If it still falls below the required minimum, new buds are added one at a time until the test is passed.

#### 7. INTERIOR BUDDING

An interior bud is generated whenever the distance between adjacent corallites exceeds the maximum intercorallite spacing, IPDIST  $\times 2.0$ . The new bud is positioned midway between flanking corallites at a growth angle that bifurcates the angle between those corallites.

#### 8. PLOTTING PROGRAM

After the entire colony is calculated by the main program, yearly growth events are plotted one at a time using the stored coordinates of the corallites. The growth surface is drawn first by connecting the  $X, Y$  coordinates in order from the vertical to the terminal corallite, with the plotting pen held down on the paper. Next, the axes of the corallites are drawn by connecting the coordinates of corallites on the new growth surface to the coordinates of those same corallites on the previous growth surface. Then, the  $X$ -coordinates of all the corallites are reversed, and the mirror image of the half-colony is plotted in the  $-X, Y$  quadrant.

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# Sponge-Zoanthid Associations: Functional Interactions

Sara M. Lewis

## ABSTRACT

Epizoic zoanthids are common in coral reef sponge communities in the West Indies. This study examines several aspects of the functional interactions between zoanthids and their host sponges. A predator inclusion experiment demonstrates that a major fish predator on the host sponge *Callyspongia vaginalis* does not discriminate between zoanthid-bearing and zoanthid-free sponges. In situ measurements of volume-specific pumping rates of sponges with and without zoanthids indicate that zoanthid colonization slightly depresses pumping rates of host sponges, and may increase sponge metabolic expenditure in an effort to overcome increased resistance. The frequencies of zoanthid colonization in two sponge species are shown to depend on size distributions of the host sponge population. This investigation suggests that the functional interactions between sponges and zoanthids vary with zoanthid species, and that the position of sponge-zoanthid associations along a parasitism-mutualism continuum depends on the particular species involved.

## Introduction

Symbiotic associations between sponges and epizoic zoanthids are common throughout shallow tropical marine environments and are particularly abundant in coral reef sponge communities. In tropical western Atlantic sponge communities, six zoanthid species occur obligately on approximately 12 common host sponge species, with varying degrees of host specificity (West, 1971; Crocker, 1977). Zoanthids become estab-

lished on a sponge following settlement and subsequent metamorphosis of one or a few planktonic larvae. Zoanthid polyps then reproduce asexually by budding and eventually colonize extensive areas of the host sponge surface. Although the systematic and morphological aspects of these associations have been described (Duerden, 1900; Crocker, 1977; West, 1979), the functional basis of the sponge-zoanthid relationship remains largely unexplored.

The present study was designed to examine directly some of the interspecific interactions that may be involved in the maintenance of the sponge-zoanthid symbiosis. Two specific hypotheses were tested: (1) avoidance of zoanthid-bearing sponges by sponge-eating fish may result in differential predation on zoanthid and non-zoanthid sponges, and (2) extensive zoanthid colonization of the inhalant surfaces of host sponges may decrease sponge pumping rates by increasing resistance to flow.

The possibility that zoanthid presence may serve to reduce fish predation on sponges was first examined by West (1976), using a single species of host sponge colonized by a brightly pigmented zoanthid species. West demonstrated not only reduced predation as a result of zoanthid colonization but also demonstrated ichthyotoxic effects of zoanthid extracts. Avoidance of zoanthid-bearing sponges by sponge-eating fish was attributed to the contrasting coloration of this sponge-zoanthid pair, with bright zoanthid pigmentation signalling toxicity to potential predators. The sponge-zoanthid pair studied by West appears to represent a mutually beneficial association whereby the sponge benefits through reduced

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predation while zoanthids are provided with a competitor-free substrate (West, 1971) in an otherwise highly space-competitive environment (Jackson and Buss, 1975). Many of the zoanthid species in the Caribbean, however, do not possess such bright pigmentation (Crocker, 1977; West, 1979), and the majority of sponge-zoanthid associations are essentially monochromatic. The lack of contrasting coloration in these associations may reflect a fundamentally different type of association. In the present study a predator inclusion experiment was conducted to determine whether zoanthid presence results in reduced predation on one of these monochromatic sponge-zoanthid pairs.

Colonization of the sponge surface by zoanthids may directly affect sponge metabolism. Zoanthid polyps colonize primarily the inhalant surfaces of host sponges, covering up to 75% of the total sponge surface (West, 1979). Partial occlusion of inhalant apertures due to zoanthid colonization may thus substantially increase resistance to water flow through the sponge, and reduce the volume of water a sponge can filter for a given metabolic expenditure. As suspension feeding in tropical water is energetically marginal (Jørgensen, 1966; Reiswig, 1974), such a reduction of pumping efficiency may be critical. In the present study, water transport rates of sponges with and without zoanthids were measured *in situ* to test the hypothesis that zoanthid colonization results in lowered sponge pumping rates.

The frequency of zoanthid colonization within a host sponge species has been studied in several locations throughout the Caribbean and has been shown to vary widely both among and within local areas (West, 1976; Crocker, 1977). Although attempts have been made to correlate these variations in colonization frequency with other biological and physical variables, the observed variations have not been satisfactorily explained. The present study surveyed the frequency of zoanthid colonization as it relates to size distribution in populations of host sponge species.

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## Materials and Methods

This study was conducted during November 1979 at Carrie Bow Cay, Belize, Central America. Two sponge-zoanthid species pairs were selected for study on the basis of their broad habitat and depth ranges, monochromatic coloration, and morphological characteristics suitable for measurements of oscular pumping rates. The sponges, *Callyspongia vaginalis* (Lamarck) and *Niphates digitalis* (Lamarck), host the zoanthid species *Parazoanthus parasiticus* (Duchassaing and Michelotti) (Figure 202) and were abundant on lagoon patch reefs and along the fore reef off Belize. For habitat descriptions and maps, see Rützler and Macintyre (herein: 9).

**PREDATOR INCLUSION.**—Relative weight loss of individuals of *Callyspongia vaginalis* with and without *Parazoanthus parasiticus* was measured in the presence and absence of fish predation in an experiment conducted adjacent to a small lagoon patch reef approximately 160 m west of Carrie Bow Cay (3 m depth). *Callyspongia vaginalis* with *P. parasiticus* was chosen on the basis of its abundance and the highly similar coloration of sponge and zoanthid tissue. Sixteen specimens of *C. vaginalis*, eight being densely colonized by zoanthids, were collected from a number of lagoon patch reefs and randomly assigned to predation and control treatments. *Pomacanthus arcuatus* (L.), the grey angelfish, was selected as a major predator because it is locally abundant in areas of high sponge density and on the basis of Randall and Hartman's (1968) observation that *C. vaginalis* constituted the single largest portion of the stomach content of this primarily sponge-feeding fish (21.9% by volume, totalled over 34 specimens). Adult fish were caught in traps, kept in a

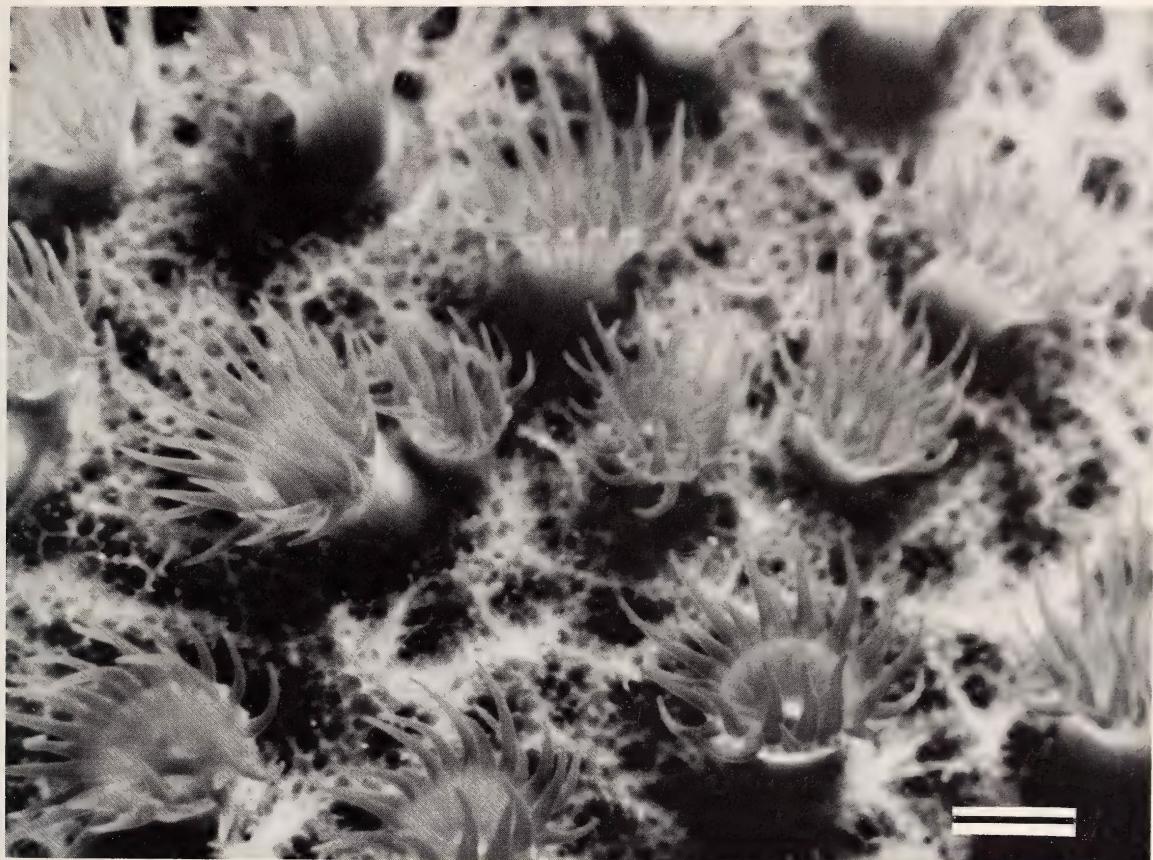


FIGURE 202.—*Parazoanthus parasiticus* on inhalant surface of *Niphates digitalis* (scale = 1 mm).

pen for one week, and starved for two days prior to the beginning of the experiment.

Sponges were weighed individually by an underwater weighing apparatus designed to balance submerged sponge weight against the buoyancy of a measured quantity of air. Because the percentage of original weight lost during the experiment was the variable of primary interest, underwater weights (expressed in ml of air) were not converted to above water weights, and changes in tissue density within a sponge during the experiment were assumed to be negligible. The precision ( $\pm 1\text{ SD}$ ) of the underwater weighing apparatus, as determined by replicate weighings of brass weights, was  $\pm 0.22\text{ ml}$  air, reflecting less than 5% of measured values.

Weighed sponges were mounted on plexiglass plates with vertical supports, and placed in two

adjacent wire mesh (2.54 cm) enclosures, one designated as a control and one with four *Pomacanthus arcuatus*, each enclosure measuring approximately  $1.5 \times 1.0 \times 0.6\text{ m}$ . An estimate of the predation pressure exerted on an individual prey in this experiment (number of predators  $\times$  number of days / included volume per individual prey) is 0.013 fish-days/liter. This predation pressure corresponds closely to that from West's (1976) predator inclusion experiment (0.010 fish-days/liter) and thus discrepancies in the results are unlikely to arise from differences in predation intensity.

The frequency of bites by *Pomacanthus arcuatus* on individual sponges was observed daily for one hour periods during the experiment. Small wrasses could move freely through the wire mesh of both enclosures, but were never observed feed-

ing on experimental sponges. Sponges were reweighed after 12 days, and the percentage of original weight lost was calculated for each individual sponge. Accurate final weights could not be obtained for a few specimens due to poor weather conditions, and one set of replicates was excluded from the analysis.

**FLOW RATES.**—Specimens of *Niphates digitalis* having a single distal atrial opening were selected for the study of water transport rates. Individual sponges were marked and measured in the field, and oscular area, atrial volume, and specimen volume were estimated by detailed measurements and geometric approximations. Axial oscular velocity (cm/sec) of each specimen was monitored for three minutes with a tripod-mounted heated-bead thermistor flow meter (LaBarbera and Vogel, 1976), enclosed in an underwater housing with a chart recorder. Volume-specific pumping rates ( $\text{cm}^3 \text{ water}/\text{cm}^3 \text{ sponge/sec}$ ) were calculated from oscular velocities (cm/sec), oscular areas ( $\text{cm}^2$ ), and sponge volumes ( $\text{cm}^3$ ). Specimens occurring with *Parazoanthus parasiticus* were chosen for their dense colonization, and zoanthid density was estimated by counts in  $0.4 \text{ cm}^2$  quadrats ( $N = 16-36$  depending on sponge size) located over the inhalant surface of the sponge.

**COLONIZATION FREQUENCY.**—The frequency of zoanthid colonization relative to sponge size was determined for two host sponge species, *Callyspongia vaginalis* and *Niphates digitalis*. The populations of each species were censused in two locations: (1) a lagoon patch reef 150 m west of Carrie Bow Cay (6 m depth) and (2) a 100 m section along the outer ridge of the fringing reef (15 m depth). Presence/absence of *Parazoanthus parasiticus* and sponge height from basal attachment to oscular rim were noted for all *N. digitalis* individuals. As *C. vaginalis* generally occurs in clusters of tubular elements, both the number of tubes and the maximum height from basal attachment were measured in order to assess sponge volume more accurately. Original measurements in inches were later converted to centimeters.

## Results

**PREDATOR INCLUSION.**—Mean percentage weight change for zoanthid and nonzoanthid *Cal-*

*lyspongia vaginalis* in control and predation enclosures is shown in Table 37. All zoanthid-bearing sponges in the control enclosure gained weight during the experiment, while all other sponges lost weight. Although both predation and zoanthid presence appear to affect weight loss in experimental sponges significantly (Table 38), examination of individual contrasts using Scheffé (1959) multiple comparison tests reveals that this differential weight loss in zoanthid and nonzoanthid sponges occurs only in the control treatment. The significant  $P$  values for both predation and zoanthid main effects, as well as the significant interaction term, derive from the marked weight gain of control zoanthid sponges. In the control enclosure, zoanthid sponges gain significantly more weight than nonzoanthid sponges ( $P < 0.001$ ); no significant difference ( $P > 0.05$ ) in mean weight loss is found between zoanthid and nonzoanthid sponges in the predation enclosure.

Daily observation of the predator enclosure could be conducted during only part of the experimental period because of poor weather conditions. These observations nonetheless indicate that *Pomacanthus arcuatus* preys on *C. vaginalis* regardless of the presence of zoanthids.

**FLOW RATES.**—Sponge height, oscular area, volume, zoanthid density, and volume-specific

TABLE 37.—Mean weight change (% of original weight) of *Callyspongia vaginalis* with and without *Parazoanthus parasiticus* enclosed with and without the predator *Pomacanthus arcuatus* ( $\pm SD$ ; three replicates per treatment)

Zoanthids	Predation		Control	
	Present	Absent	Present	Absent
Present	$-17.7 \pm 12.8$		$+33.0 \pm 3.5$	
Absent	$-10.2 \pm 7.3$		$-11.9 \pm 12.5$	

TABLE 38.—Two-way analysis of variance on percentage weight loss in *Callyspongia vaginalis* with and without *Parazoanthus parasiticus* enclosed with and without *Pomacanthus arcuatus*

Source	df	MS	F	P
Predation	1	1793.41	12.43	0.0078
Zoanthid presence	1	1050.94	7.29	0.0271
Interaction	1	2056.70	14.26	0.0054
Error	8	144.25		

TABLE 39.—Measurements on *Niphates digitalis* specimens concerning dimensions, zoanthid presence and density, and volume-specific pumping rates

Sponge number	Height (cm)	Oscular area ( $\text{cm}^2$ )	Volume ( $\text{cm}^3$ )	Zoanthid density ( $\bar{X} \pm SD$ ) (no./ $\text{cm}^2$ )	Pumping rate ( $\text{cm}^3 \text{ water}/\text{cm}^3 \text{ sponge/sec}$ )
ON18	27.9	17.3	338	5.9±.9	0.16
ON10	17.8	97.9	549	4.3±.7	0.28
ON15	18.4	10.0	184	4.1±1.0	0.16
ON20	22.2	43.3	472	5.1±.7	0.02
ON19	17.1	50.5	355	4.7±1.0	0.19
ON16	14.0	50.7	173	4.3±.8	0.23
ON1	14.0	66.4	309	0	0.60
ON12	27.9	45.7	504	0	0.25
L6	29.2	94.8	639	0	0.16
ON14	29.2	27.1	616	0	0.13
ON11	24.1	40.9	764	0	0.11

pumping rates are given in Table 39 for 11 specimens of *Niphates digitalis*. Mean pumping rates for *N. digitalis* with and without *Parazoanthus parasiticus* (Table 40) indicate pumping rates for both groups of sponges within the range reported by Reiswig (1974) for three taxonomically distant sponge species. The mean pumping rate of non-zoanthid sponges is higher than that of zoanthid-bearing sponges, although not significantly so ( $P > 0.05$ , *t*-test for means with unequal variances on log-transformed variates). Sponges without *P. parasiticus* show greater among-sponge variance in pumping rates than do zoanthid-bearing sponges ( $0.025 < P < 0.05$ , *F*-test). Zoanthid densities averaged over the entire sponge surface show no correlation with pumping rates ( $P > 0.05$ , Kendall's rank correlation).

**COLONIZATION FREQUENCY.**—For a given location, the frequency of zoanthid colonization appears to be related closely to sponge size. Plots of sponge height versus number of tubes for each specimen of *Callyspongia vaginalis* from the lagoon patch reef and outer ridge populations (Figure 203) indicate that the largest individuals in both populations generally occur with *Parazoanthus parasiticus*, while smaller individuals have lower colonization frequencies.

Size (here represented only by sponge height) vs. frequency distributions of *C. vaginalis* in the two locations (Figure 204) indicate that the lagoon population consists of sponges of greater

height with a lower proportion of small individuals than the outer-ridge population. This difference may reflect lower recruitment rates and an older, or possibly a faster-growing, population in the lagoon. Colonization frequency is significantly related to *C. vaginalis* height at both locations (lagoon,  $P < 0.01$ ; outer ridge,  $P < 0.005$ , *G*-tests (log likelihood ratio) used for all frequency comparisons, with continuity correction for small sample size where appropriate). In the lagoon colonization frequencies range from 0% for the 0–16 cm size classes to 47% for the size classes greater than 31 cm. In the outer-ridge population, colonization frequencies for the same size classes are 33% and 93%, respectively.

Comparisons of colonization frequencies between the outer-ridge and lagoon populations for both sponge species grouped by size class (Table 41) indicate significantly higher colonization frequencies for *C. vaginalis* on the outer ridge for each size class ( $P < 0.025$  for all size classes). The overall (summed over all size classes) colonization

TABLE 40.—Volume-specific pumping rates ( $\text{cm}^3 \text{ water}/\text{cm}^3 \text{ sponge/sec}$ ) for *Niphates digitalis* with and without *Parazoanthus parasiticus*

Zoanthids	<i>N</i>	Pumping rate ( $\bar{X} \pm SD$ )
Present	6	0.173±0.080
Absent	5	0.250±0.181

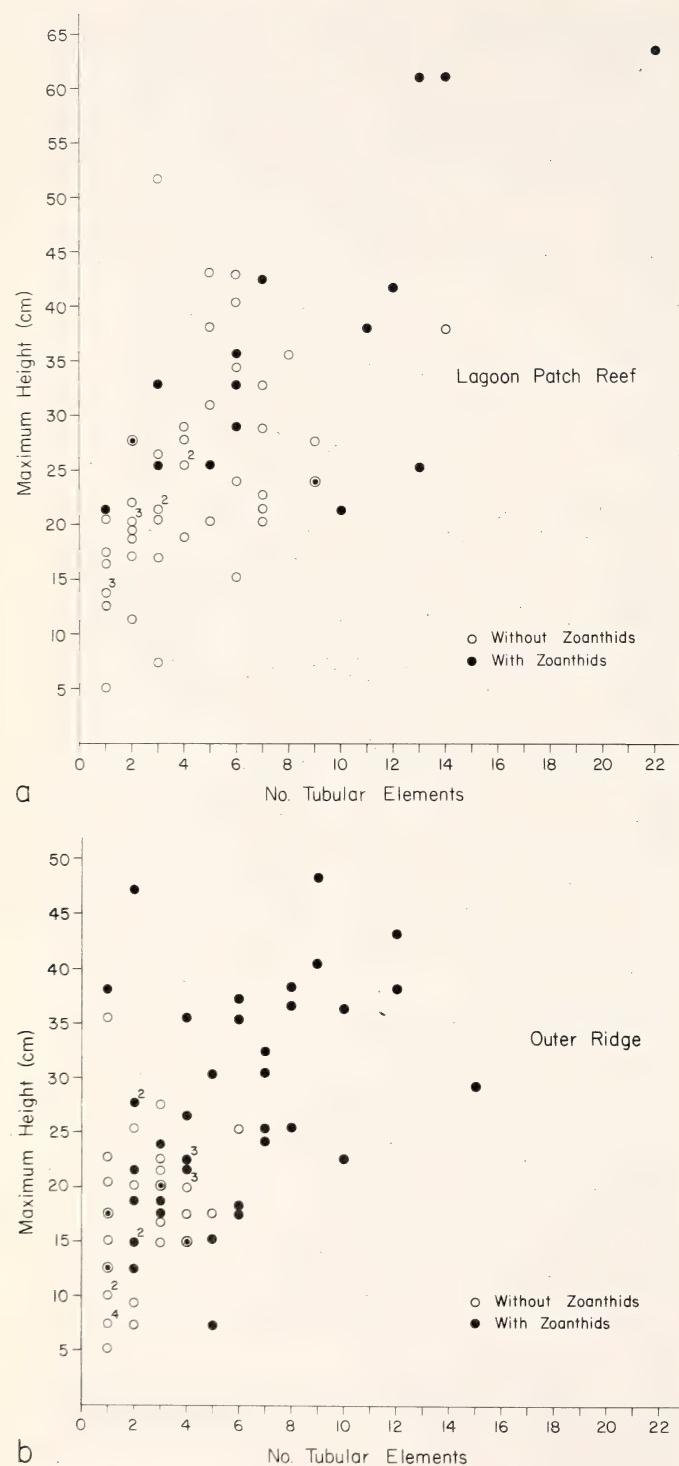


FIGURE 203.—*Callyspongia vaginalis*, sponge height versus number of tubes for individuals with and without *Parazoanthus parasiticus*: a, lagoon patch reef; b, outer ridge. (Multiple values indicated.)

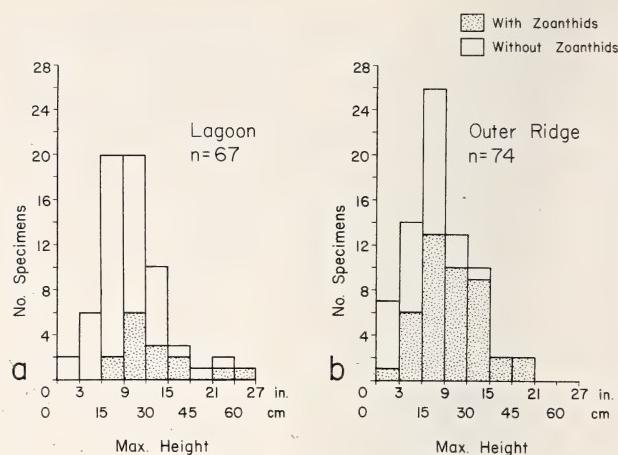


FIGURE 204.—*Callyspongia vaginalis*, size-frequency distributions: a, lagoon patch reef population; b, outer ridge population. (Original measurements in inches).

frequency of 83% in the outer-ridge population is significantly higher than that of 25% in the lagoon ( $P < 0.005$ ). No significant differences were found between locations for any size class of *N. digitalis* (Figure 205), and there was no significant difference in overall colonization frequencies between the two locations (32% lagoon, 38% outer ridge).

## Discussion

**PREDATOR INCLUSION.**—The predator inclusion experiment clearly demonstrates that the sponge predator *Pomacanthus arcuatus* does not distinguish between *Callyspongia vaginalis* with or without *Parazoanthus parasiticus*. This finding is contrary to results of previous work with *Holacanthus tricolor* (Bloch) preying on the sponge *Iotrochota birotulata* (Higgin) with *Parazoanthus swiftii* (Duchassaing and Michelotti) (West, 1976), where the presence of zoanths appeared to reduce predation on experimental sponges. Intraperitoneal injection of extracts of two zoanths, *P. swiftii* and *P. puerto-ricense* West, both highly pigmented species, provided evidence for zoanthid toxicity to fish (West, 1976). The avoidance of zoanthid-bearing sponges by predators was further shown by West to be visually mediated, although the effects of zoanthid coloration were not distinguished from those of zoanthid shape. The bright pigmentation

TABLE 41.—Colonization frequencies of *Callyspongia vaginalis* and *Niphates digitalis* comparing lagoon patch reef and outer ridge populations (*P* values are given for *G*-tests of association between colonization frequency and location within size class)

Size class (cm)	Location	Number of individuals			Colonization frequency (%)	<i>P</i>
		With zoanthids	Without zoanthids	Total		
<i>Callyspongia vaginalis</i>						
0-23.0	Lagoon	2	26	28	7.1	<0.005
	Outer ridge	20	27	47	42.5	
23.1-31.0	Lagoon	6	14	20	30.0	<0.025
	Outer ridge	10	3	13	76.9	
>31.0	Lagoon	8	9	17	47.1	<0.025
	Outer ridge	13	1	14	92.9	
<i>Niphates digitalis</i>						
0-16.0	Lagoon	2	8	10	20.0	>0.05
	Outer ridge	9	29	38	23.7	
16.1-23.0	Lagoon	2	6	8	25.0	>0.05
	Outer ridge	7	8	15	46.7	
>23.0	Lagoon	6	7	13	46.2	>0.05
	Outer ridge	11	8	19	57.9	

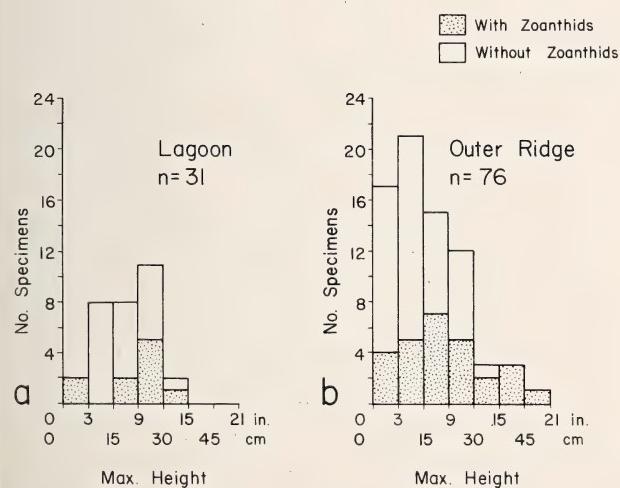


FIGURE 205.—*Niphates digitalis*, size-frequency distributions: *a*, lagoon patch reef population; *b*, outer ridge population. (Original measurements in inches).

of *P. swiftii* was interpreted as warning coloration signalling zoanthid toxicity to potential predators. Although toxicity of the remaining zoanthid species has not been tested, the results of the present experiment with *P. parasiticus* strongly suggest that the lack of zoanthid pigmentation and contrasting coloration in many sponge-zoanthid pairs may be related to a lack of protection

of host sponges from fish predators.

Three of the zoanthid species known from the Caribbean, *P. swiftii*, *P. puertoricense*, and *Epizoanthus cutressi* West, are highly pigmented (West, 1979). The remaining species, *P. parasiticus*, *P. catenularis* (Duchassaing and Michelotti), and *Epizoanthus* sp. (see Crocker, 1977:32 for description), are greyish white and blend nearly completely with the color of their host sponges. The present study suggests the existence of two classes of sponge-zoanthid associations. The first group, comprised of brightly pigmented zoanthids and their host sponge species, may represent mutualistic associations in which the presence of toxic zoanthids serves to reduce predation on host sponges. In the second group dull coloration, which may be correlated with a lack of toxicity, appears to indicate a lack of protection of host sponges from predation. If two such classes of sponge-zoanthid associations do exist, the evolutionary development of zoanthid toxicity as a means of reducing predation on the sponge-zoanthid complex may represent the crossover point from an essentially parasitic association, in which no benefit to the sponge can be identified, to a mutualistic one.

The significant weight gain of zoanthid-bearing sponges relative to nonzoanthid sponges in the control treatment of the present experiment remains unexplained. West (1976) reports a similar result with *Iotrochota birotulata*; in his control treatment, zoanthid-bearing sponges have a reduced weight loss compared to nonzoanthid sponges. The significance of the difference, however, was not tested and sufficient data are not given for such tests to be performed now. This differential weight change within the control treatment is important in that it may bias experimental results in the direction of finding lower weight loss in zoanthid-bearing sponges in other treatments, thus it should have been considered in the analysis of West's results. The weight gain of zoanthid-bearing sponges in the present experiment may reflect increased growth rates in zoanthid-bearing sponges relative to nonzoanthid sponges, although it is also possible that zoanthid growth compensates sponge weight loss. The possibility of differential growth rates of zoanthid-bearing and nonzoanthid sponges is currently under investigation in natural populations.

Previous studies of sponge population dynamics have shown that predation by fishes is a negligible source of mortality (Reiswig, 1973, in Discovery Bay, Jamaica). Field observations of *Pomacanthus arcuatus* at Carrie Bow Cay, however, clearly indicate predation on *Callyspongia vaginalis* in fore-reef areas (S. M. Lewis, unpublished observations). In addition, sponges with extensive tissue loss, presumably resulting from predation, are common in sponge populations on the fore reef. The depauperate sponge-eating fish fauna in Discovery Bay, the result of intensive trap-fishing along the northern coast of Jamaica, may be responsible for an underestimate of fish predation in sponge populations in other areas of the Caribbean. Further work is needed to quantify the effects of fish predation on sponge populations.

**FLOW RATES.**—*Parazoanthus parasiticus* extensively colonizes the inhalant surfaces of *Niphates digitalis*, and polyps may completely or partially block inhalant apertures. Zoanthid colonization

may be expected to cause an increased resistance to water flow through the sponge, assuming the number of ostia remains constant. The lower mean volume-specific pumping rate observed in zoanthid sponges may be evidence of this overall depression of water transport rates due to zoanthid colonization. If, however, choanocyte pumping activity can be increased to compensate for increased resistance, pumping rates of zoanthid and nonzoanthid sponges may appear similar. The major observed difference in pumping rates between zoanthid and nonzoanthid sponges appears in the significantly lower variance among zoanthid sponges. This reduced variance may indicate that these sponges are uniformly increasing their choanocyte activity to its physiological limit in order to compensate for increased resistance due to zoanthid colonization. This would be expected to increase metabolic expenditure, without increasing filtration rate, and would thus have a significant effect on sponge maintenance metabolism, as well as on the energy available for growth and reproduction.

**COLONIZATION FREQUENCY.**—Previous studies of sponge-zoanthid associations in the Caribbean have included observations of the frequency of zoanthid colonization and have established the variability of colonization frequencies among host sponge populations in different locations. West (1976) noted that the colonization frequency of *Iotrochota birotulata* by *Parazoanthus swiftii* in shallow water (<3 m) near La Parguera, Puerto Rico, was low, whereas in deeper water colonization frequency was close to 100%. He suggests that this difference may be related to fish predator abundance, although neither colonization frequency nor predation intensity was quantified. Crocker (1977) determined zoanthid colonization frequencies for 10 host sponge species in four transects along the outer bank reef off the west coast of Barbados. Colonization frequencies for *I. birotulata* with *P. swiftii* in these transects were low, ranging from 0% ( $N = 51$ ) to 8% ( $N = 422$ ), while the colonization frequency for *Callyspongia vaginalis* with *P. parasiticus* ranged from 59% ( $N = 22$ ) to 76% ( $N = 42$ ). Within sponge species no

correlation was found between colonization frequency and host sponge density in transect areas; also, overall colonization frequency (summed over all host sponge species) was not related to water depth.

The present study demonstrates that any attempt to explain variations in colonization frequency among host sponge populations must first take into account the size distribution of host sponges within the populations. For both *Callyspongia vaginalis* and *Niphates digitalis* in two distinct physiographic areas, colonization frequency has been shown to be directly related to sponge size. Within a given location, size may be assumed to be some monotonically increasing function of sponge age. The correlation of colonization frequency with sponge size appears to indicate an increase in the cumulative probability of zoanthid larval settlement with sponge age, although the possibility of increased survivorship and/or growth rate of zoanthid-bearing sponges cannot be excluded. This dependence of zoanthid colonization frequency on sponge size may be responsible for some of the differences in colonization frequencies reported in previous studies, as overall colonization frequency will clearly depend on the size distribution of the population under study.

The significant difference in colonization frequencies observed in the present study between *Callyspongia vaginalis* on the outer ridge and the lagoon cannot be attributed to differences in the population size structure between locations, as comparisons within all size classes give the same result. This difference in colonization frequency is not likely to be mediated by differences in predator abundance between locations, as suggested by West (1976), because of the demonstrated lack of discrimination between zoanthid and nonzoanthid *C. vaginalis* by fish predators. A number of mechanisms might be responsible for the observed difference. The outer ridge may have higher *Parazoanthus parasiticus* larval availability or higher rates of successful zoanthid settlement and/or metamorphosis, although the lack of significant differences in colonization frequencies between locations for *Niphates digitalis* sug-

gests uniform *P. parasiticus* availability. An alternative explanation, assuming equal larval availability and settlement in both locations, would be reduced growth rates of *C. vaginalis* on the outer ridge relative to the lagoon population. Individuals of a given size on the outer ridge would then have been exposed to zoanthid settlement for longer periods of time than similarly sized, but younger, individuals in the lagoon. Thus either differential rates of successful zoanthid settlement and metamorphosis on host sponges or differential sponge growth rates in *C. vaginalis* populations may explain the observed difference in colonization frequency between the two locations.

### Conclusions

Although the present study has considered only a subset of the possible interactions between sponges and epizoic zoanthids, some aspects of the nature of the association have been elucidated. Rates of predation on zoanthid and nonzoanthid sponges by a major fish predator appear to be identical for *Callyspongia vaginalis* and *Parazoanthus parasiticus*, a common species pair representative of sponge-zoanthid associations lacking contrasting coloration. Zoanthid colonization appears to slightly depress sponge pumping rates. Reduced variance of pumping rates among zoanthid sponges implies an increased metabolic expenditure to maintain pumping rates against increased resistance. Zoanthid colonization frequency has been shown to increase with sponge size within a host sponge species. Comparisons of colonization frequencies between sponge populations must take into account potential differences in the age structures of the populations.

The obligate nature of the sponge-zoanthid association for the six zoanthid species found in the tropical western Atlantic indicates a net benefit to symbiotic individuals relative to hypothetical free-living precursors. Perhaps the most obvious advantage to the zoanthids is the availability of competitor-free substrate for colonization. There appear to be two classes of sponge-zoanthid associations, distinguished on the basis of whether zoanthid presence provides a reciprocal net bene-

fit to the host sponge through reduced predation. Increased resistance to water flow due to zoanthid colonization may result in a reduction of energy available for sponge maintenance, growth, and reproduction. In some sponge-zoanthid associations, zoanthid toxicity appears to reduce predation on zoanthid-bearing sponges, and may thus result in increased survivorship and reproductive output relative to nonzoanthid sponges. The development of toxicity and bright pigmentation

by some zoanthid species may be a physiological investment serving to increase the survival of the host sponge, and may represent a crossover from parasitic to a mutualistic association. Additional study of growth rates, survivorship, reproductive output, and competitive abilities of zoanthid-bearing and nonzoanthid sponges is needed in order to determine precisely the position of particular sponge-zoanthid associations along a parasitism-mutualism continuum.

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# On the Ecology of *Isaurus duchassaingi* (Andres) (Cnidaria: Zoanthidea) from South Water Cay, Belize

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## ABSTRACT

On the shallow, wave-exposed reef crest of South Water Cay, Belize, more than 700 *Isaurus duchassaingi* polyps were found aggregated in adjacent clumps of up to 100 or more animals each, altogether covering nearly 3 m<sup>2</sup> of coral rubble and algal substrate. Phenotypic variability of polyps is evident from differences in column and capitulum coloration and tubercle size and arrangement. Asexual reproduction by budding from anastomotic stolons or coenenchyme predominates, although hermaphroditic and female polyps are also present. Behavioral and morphological adaptations enable the zoanthids to exist within a harsh, fluctuating environment. The zoanthids display nocturnal activity by expanding their columns and tentacles only after dusk. Light and food stimuli cause the tentacles to retract quickly. Rather than microscopic zooplankton, macroscopic prey (that is, larval fish) may form the diet. Nutritional requirements of *Isaurus* spp. probably depend on both zooxanthellae and exogenous food transported by waves.

## Introduction

Zoanthids of the genus *Isaurus* have circum-tropical distributions and live inconspicuously among rocky-coral substrates. Although isolated

colonies of 5 to 8 polyps occur at depths to 20 m (C. Arneson, pers. comm., 1979), most *Isaurus* species are more abundant in intertidal areas. This is the first report on the ecology and behavior of the Caribbean zoanthid *Isaurus duchassaingi* (Andres, 1883). This study also extends its known range to the continental region of Central America, near Carrie Bow and South Water cays, Belize. Hitherto, *I. duchassaingi* was reported from the following West Indies locations: St. Thomas and Guadeloupe (Duchassaing and Michelotti, 1864), Bahamas (McMurrich, 1896), Jamaica (Duerden, 1898), and Puerto Rico (Duerden, 1902).

Related species are known from similar tropical habitats in the Indian, Pacific, and Atlantic oceans (Andres, 1877; McMurrich, 1889; Haddon and Shackleton, 1891; Verrill, 1928; Carlgren, 1938; Herbersts, 1970, 1972a, 1972b; Day, 1969; Walsh and Bowers, 1977). Species of *Isaurus* have variable morphological features: growth habit, color, size, number and shape of tubercles on the column, and internal anatomy and cytology. The only previous ecological study of these zoanthids was done by Herbersts (1972a), who examined habitat requirements for *Isaurus spongiosus* (Andres) from Madagascar; she found that rubble substrate, some degree of dampness, and strong currents were principal distributional factors.

The objectives of this study were to examine ecological parameters, morphological variation, relative abundance and distribution, reproduc-

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tive biology, functional morphology, zooxanthellae symbionts, general day and night behavior, feeding methods, and prey selection on the basis of both field and laboratory observations of *Isaurus duchassaingi*. Numerous colonies partly concealed among coral rubble were found in an algal zone at the northeast reef crest on South Water Cay, just north of Carrie Bow Cay. A few colonies were also seen on the fore-reef terrace east of Carrie Bow Cay. A nocturnal species, *I. duchassaingi* has been illustrated only in retracted, diurnal postures (Duchassaing and Michelotti, 1860, 1864; McMurrich, 1896; Duerden, 1898, 1902). This paper illustrates the expanded animal at night with tentacles exposed.

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## Materials and Methods

*Isaurus duchassaingi* occurs in small numbers on the reef terrace of Carrie Bow Cay, but is most abundant on the northeast reef crest of South Water Cay, a 28 km<sup>2</sup> island about 1.5 km north of Carrie Bow Cay, Belize (Figure 206a). The distribution of these colonies was mapped in March 1978 with the aid of metal poles as markers, compass, and measuring tape. Distances between colonies, estimated numbers of animals and their color, and habitat were described and photographically recorded. Conspicuous associated organisms, if visible without disturbing the community, were also recorded.

Two single animals and more than 30 adult polyps from one colony of *Isaurus duchassaingi* were collected with their substrate attached and were kept for over three weeks in shaded aquaria. The animals were covered by 15 cm of nonrunning

sea water, which was changed daily. Morphological features of *I. duchassaingi* were noted during the day. Laboratory observations at night were made by direct light and by subdued indirect light from a flashlight; specimens were photographed with a prefocused camera and electronic flash. Feeding experiments were conducted in outside aquaria at night after the animals had been expanded for two hours. Live zooplankton, lab-cultured brine shrimp, or 1 mm<sup>3</sup> pieces of fresh fish were fed to the animals by dropping them from forceps or pipette onto the tentacles. Live crab zoeae and 12 mm long fish were also kept overnight with the zoanthids.

Preserved polyps were dissected and examined under low magnification. Transverse sections through the column below the actinopharynx, including gonads and mesenterial filaments, were prepared for microscopic examination. Histological sections (6 µm) of paraffin-embedded tissue were stained with Hematoxylin-Eosin. Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

## Results

**STUDY SITE.**—South Water Cay is a sparsely populated island, about 400 m long by 80 m wide, located at 16°49'N, 88°05'W, east-southeast of Belize City, Central America (Figure 206a). Leeward of the island is a seagrass-covered lagoon, 0 to 8 m deep. Windward there is a shallow (0 to 0.5 m deep) muddy sand and mixed seagrass reef flat extending 25 to 100 m to the reef crest. At the northeastern end of the island, the storm-rubble reef crest, about 50 m wide, meets the shore (Figure 207a).

*Isaurus duchassaingi* is found in greatest numbers at the northeastern end of South Water Cay. Here the entire reef crest is strewn with large dead coral boulders 0.5 m or more in height (Figure 206b, Zones 1-4). The substrate changes from near-shore mud and sand (Zone 1) to a compact, diffusely intermeshed cobbled area toward the middle of the crest (Zone 2), to rubble

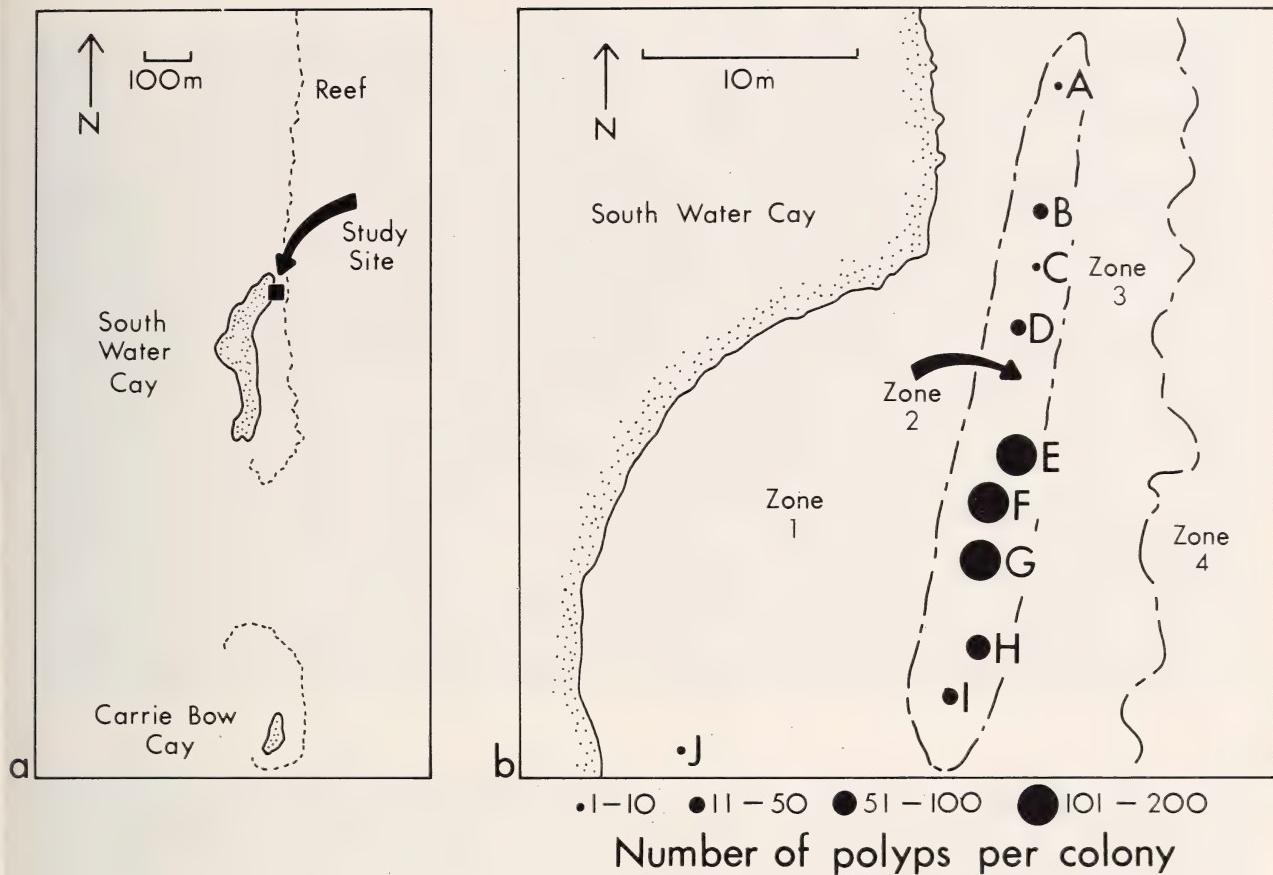


FIGURE 206.—Maps of study area: *a*, South Water Cay and Carrie Bow Cay, Belize, showing study site; *b*, study site NE of South Water Cay showing zonation of reef crest and location and abundance of *Isaurus duchassaingi* colonies (A–J). Zones: (1) *Zoanthus sociatus*; (2) algal belt with *Isaurus duchassaingi*; (3) *Porites astreoides*; (4) *Diadema antillarum* and *Palythoa* sp.

and beach rock seaward (Zones 3 and 4). About 10 to 15 m from shore (Zone 2), various algae growing in a yellow-green turf over the rubble form an approximate north-south extended algal belt, about 33 m long and 4 m wide. The belt is composed mainly of the Chlorophyta *Cladophoropsis membranacea* (C. Agardh), with associated Chlorophyta: *Halimeda* sp. and *Dictyosphaeria* sp.; Rhodophyta: *Laurencia* sp., *Hypnea* sp., *Lophosiphonia* sp., *Gelidiella* sp. and *Jania* sp.; and Phaeophyta: *Padina* sp.

Average 20 cm tides and predominant northeast trade winds markedly affect the crest biota. At extreme low tides the area is exposed for more than six hours; at mean high tides near-shore

substrate is covered by 10 cm or more of water, and the low tide wave line is covered by 30 cm. Waves paralleling the shoreline break harshly over the crest on incoming tides.

Throughout the region opposite the indented shore, invertebrates are distributed in distinct areas (Figure 206*b*, Zones 1–4). Conspicuous sessile animals observed near shore (Zone 1) are scattered colonies of the green zoanthid *Zoanthus sociatus* (Ellis) associated with sabellid polychaetes, and the orange or brown burrowing anemone *Actinoporus elegans* Duchassaing. In the algal belt (Zone 2), colonies of *Isaurus duchassaingi* are clumped in patches or scattered singly among coral debris that is channeled by sipunculids and



FIGURE 207.—Views of Zone 2: *a*, rubbled reef crest from shore at South Water Cay, algal belt lies in front of wave line; *b*, close-up view of a small *Isaurus duchassaingi* colony on coral within the algal belt; scale at bottom in mm.

polychaetes. Other colonies are found at the bases of coral boulders that are sometimes capped by the ribbed barnacle *Tetraclita* sp. Within 5 m seaward of the algal zone, heads of the coral *Porites astreoides* Lamarck are interspersed among the rubble (Zone 3). Eastward (in Zone 4), there are numerous *Diadema antillarum* (Philippi) (Echinoidea), clumps of *Palythoa* sp. (Zoanthidea) and scattered *Stoichactis helianthus* (Ellis) (Actiniaria). Beyond Zone 4, coral growth flourishes and is dominated by the coral *Acropora palmata* (Lamarck). (For coral distribution see Rützler and Macintyre, herein; Cairns, herein).

**FIELD OBSERVATIONS.**—At the study site, 10 colonies or patches of *Isaurus duchassaingi* comprising well over 700 polyps covering approximately 3 m<sup>2</sup> were found in the algal belt. Estimated number of animals per colony varied from two to 200; it was impossible to count all the polyps without digging colonies from the substrate. A clump of 100 or more animals covered approximately 400 cm<sup>2</sup>. The colonies were densest at the center of the belt, where more than 550 polyps were within 7 m of each other (Figure 206b, Zone 2, E-G). The four northernmost (Figure 206b, Zone 2, A-D) and three southernmost colonies (Figure 206b, Zone 2, H-J) had less than 200 polyps combined and less than 10 animals per patch at sites farthest from the dense central population.

In the algal belt, *Isaurus duchassaingi* colonies are most easily located when they are emerged at low tide. Isolated forms, some solitary, but most of them colonial (aggregate, adjacent clumps of 3 to 8 polyps growing from a common stolon or coenenchyme), are abundant on a slightly raised area of the reef crest. The only visible part of the animal is the gibbose, distal portion of the tuberous column—from 1.5 to 2.5 cm in length and 6 to 8 mm in diameter—which blends well with the green and brown algal growths, encrusting coralline algae, and assorted worm tubes on dead, pitted coral pieces (Figure 207b). The lower columns of the animals are hidden, wedged between, or half buried beneath, the coral.

Colonies are united below the substrate by

holdfasts of anastomotic stolons and coenenchyme bases of adult polyps adhering to one or more pieces of coral. Embedded around the coenenchyme and stolon tracts are calcareous sand grains, *Halimeda* chips, sea urchin spines, and *Homotrema rubra* (Lamarck) (Foraminifera) tests. Because the lower side of the coral substrate is partially covered with bryozoans, serpulid tubes, and *H. rubra* nodules, the zoanthid bases partially overgrow these organisms.

The color of the exposed part of the polyp columns varies from grey-green to brown to yellow. In the algal belt, where the colonies are densest (Figure 206b, Zone 2, E-G), all animals are olive-grey, mottled with metallic turquoise. Animals in smaller colonies to the north have group colors varying from green-tan to brown-gold with or without a light turquoise hue (Figure 206b, Zone 2, A-D). The southernmost colonies in the belt are either all dark brown with yellow-tan knobs—a few polyps are speckled with turquoise (Figure 206b, Zone 2, I)—or are all tan-yellow (Figure 206b, Zone 2, H, and Zone 1, J). Only the basal 1.5 to 2.0 cm, unexposed lower column is partly beige or whitened like the stolon and the younger polyp buds below.

**LABORATORY OBSERVATIONS.**—At dusk, in an aquarium, with the animal straightened and capitulum in view, the external column morphology of *Isaurus duchassaingi* is easily discernible (Figure 208). The tubercled columns of the animals may or may not be transversely wrinkled. In some colonies, a thin cuticular sheath sloughs from the unincrusted column and minute algal tufts cling to the capitular and basal regions. The capitular disc has numerous radiating ridges and furrows that are the same color as the column, or has about 15 or fewer white streaks (Figure 208b). The base of each polyp lacks tubercles and is firmly adhered to one or more pieces of coral.

The rest of the polyp, except for the unexposed, proximal portion, has variously shaped tubercles, which may or may not be contiguous, arranged in longitudinal or transverse ridges around the column. The most distal tubercles on the column (crown tubercles) are arranged in a partial or

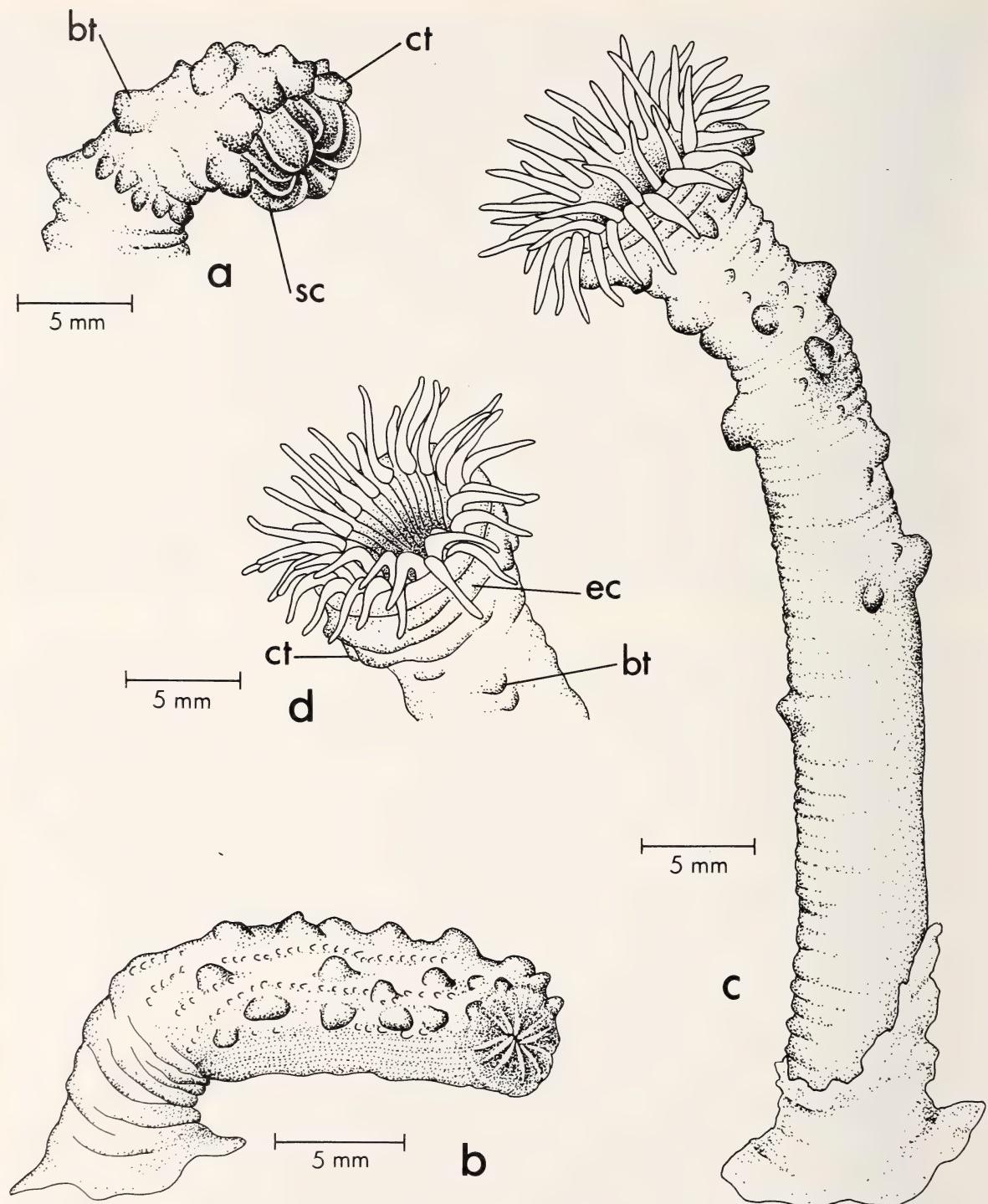


FIGURE 208.—*Isaurus duchassaingi* live habit: *a*, contracted, swelled capitulum; *b*, contracted during the day, with closed capitulum; *c*, expanded at night, with tentacles exposed; *d*, extended capitulum. (bt = body tubercles, ct = crown tubercles, ec = extended capitulum, sc = swelled capitulum.)

complete peripheral circle adjoining the capitular disc. The distribution and size of the tubercles on both the column and crown vary from polyp to polyp. Generally, each polyp has a modified radial symmetry around the oral-aboral axis of the column that gives the animal a bilaterally symmetrical appearance. The convex portion of the polyp usually contains most of the larger tubercles, whereas the semi-transparent concave part is smooth, or has scattered or linear series of smaller tubercles.

Column tubercles on the convex side of a polyp may be distributed randomly, or in rows, or both, as follows: the tubercles may be arranged in 3 to 4 main rows of 7 to 12 or more prominent tubercles per row, with variously sized scattered tubercles in between; or there may be merely about 15 prominent tubercles scattered sparsely on the column. A third pattern of tubercle arrangement occurs alone in some polyps or may be incorporated with either of the other tubercle distribution patterns on other polyps. In this third pattern there may be more than 8 tiny tuberculate or larger knoblike rows, each with about 10 to 20 tubercles per row, resembling kernels of corn on a cob.

Crown tubercles, 3 to 15 or more in number, may or may not be prominent. Similar-sized tubercles may extend completely around the capitular disc or only partially around the disc on the convex part. Or the tubercles may extend all around the disc, but decrease in size on the concave portion. Crown and column tubercles vary in size from 0.5 to 2.0 mm projections, and in shape from tiny verrucae to more alated protuberances.

At night, with polyps fully expanded and capitula unfolded to reveal the tentacles, the column wall extends 3 mm or more above the crown tubercles and increases the oral diameter of the peripheral capitular edge to more than 1 cm (Figures 208d, 209b). This edge supports a double circle of alternating simple, short, acuminate, white marginal tentacles that expand to more than 5 mm in length in a flabellate array. The exocoelic tentacles drape slightly downward over

the edge of the capitulum or they hang vertically downward near the column wall, whereas the endocoelic tentacles extend obliquely outward, about 90° from the exocoelic ones or droop next to the exocoelic tentacles (Figures 208c,d, 209b). All tentacles are about the same length. From photographs and observations of an expanded polyp, a diagrammatic sagittal view has been sketched to show the outstretched tentacles above an elongate preoral chamber, which probably serves as an enlarged basin to contain prey before it enters the actinopharynx (Figure 209b).

In the laboratory, *Isaurus duchassaingi* expelled zooxanthellae in mucus-covered packets, about 1 mm in diameter, which appear as brown rings surrounding a bright green center; the mucus was teaming with ciliates. Photographs show the endoderm of the tentacles with numerous brownish green zooxanthellae.

The behavior of colonies in aquaria during the day is similar to that of colonies observed in the field at low tide. During the day, polyps are arched toward the substrate and the closed capitulum is oriented downward or perpendicular to the ground (Figures 207b, 208b). Polyp orientation is random with regard to waves. By dusk (1830 h) polyps expand their hook-like columns somewhat and inflate the capitulum (Figure 208a), but this movement is too gradual to be seen. By 2000 h, many of the polyps are vertically expanded 4 to 5 cm or more above the substrate, having increased their column lengths by about 1 cm; their columns may be straight or slightly curved, and may be sustained in an erect or angled posture; their capitula are open and tentacles exposed (Figure 208c).

At night during the first two weeks in aquaria, the polyps reacted to direct light by retracting all tentacles and closing the preoral cavity within two seconds. No noticeable contraction of the column occurred. The tentacles reexpanded within three hours after the direct light was extinguished. In the third week, when subjected to direct light, the zoanthids did not close until two to three minutes later, for unknown reasons.

During feeding experiments observed with

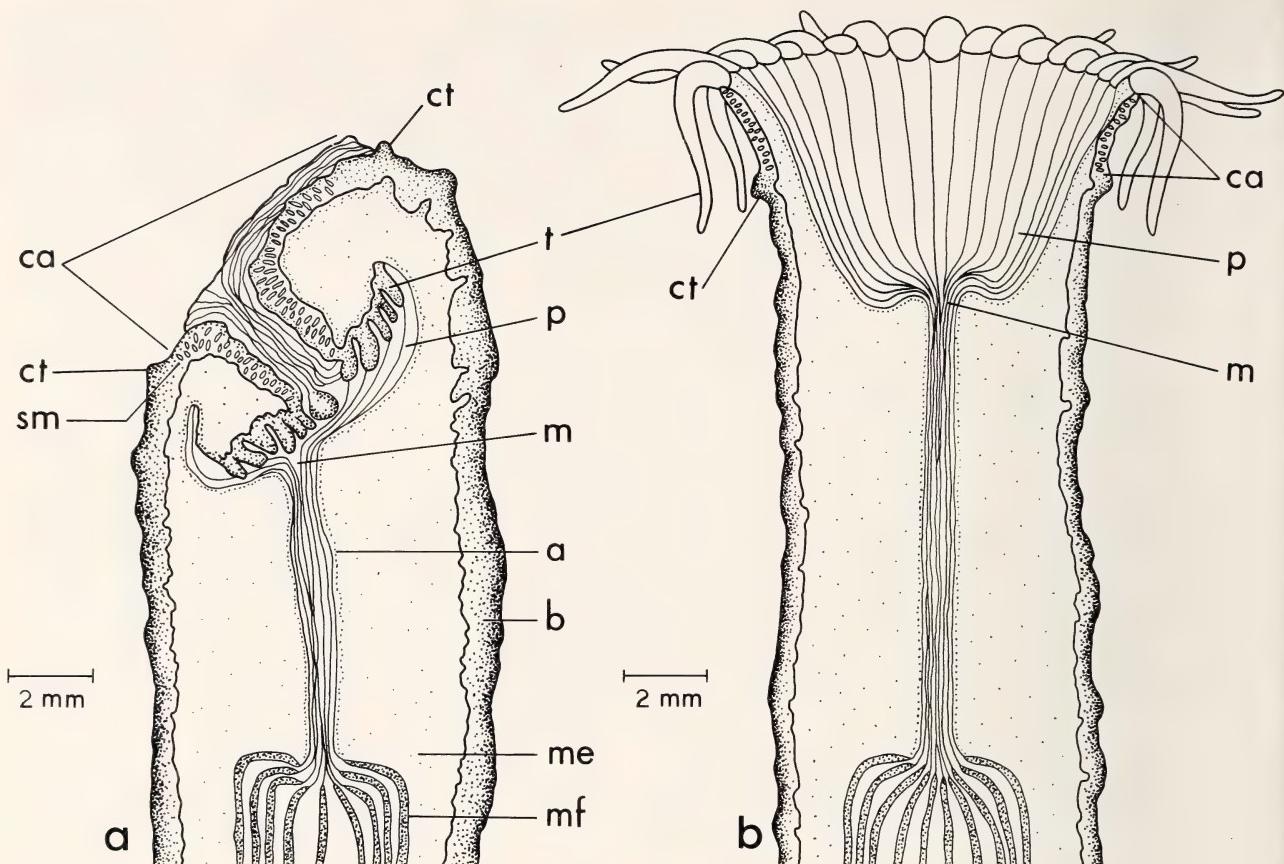


FIGURE 209.—*Isaurus duchassaingi*, median sagittal sections through anterior portion of polyp: *a*, preserved, retracted; *b*, live posture, expanded (diagrammatic). (*a* = actinopharynx, *b* = body wall, *ca* = capitulum, *ct* = crown tubercles, *m* = mouth, *p* = preoral chamber, *me* = mesentery, *mf* = mesenterial filaments, *sm* = sphincter muscle, *t* = tentacle.)

minimal light, *Isaurus duchassaingi* closed its preoral cavity as soon as food touched the tentacles. A piece of fresh fish less than  $1 \text{ mm}^3$  dropped onto the tentacles caused the tentacles and capitulum to infold completely with the food within three seconds. When live microzooplankton was gently pipetted onto the tentacles or preoral cavity, some of it was caught. Live isopod crustaceans dropped into the cavity usually escaped, except for some of the less active ones, which became enclosed in the chamber when the capitulum folded. Brine shrimp, *Artemia salina* (Linnaeus), were quickly caught on the tentacles, which then retracted into the chamber. Whether these prey were digested was not observed. When a 10 mm long cardinal fish touched the tentacles of a polyp

that had previously been starved for a week, the fish adhered and was immediately transferred into the chamber, which closed as the tentacles simultaneously folded in. The following morning, the zoanthid had ejected a bolus, indicating that the fish had been digested, the process taking less than 12 hours.

Because it took several hours for *Isaurus duchassaingi* to reexpand after a disturbance by feeding or photographing, only one feeding experiment could be done each night. Potential food organisms, however, were allowed to swim freely overnight in the same aquarium. For several days, three trigger fish about 12 mm in length swam near the zoanthids but were not eaten. Likewise, crab zoeae left in aquaria overnight with these

zoanthids were not captured, even though, owing to their erratic movements, they probably swam into the tentacles. A small gastropod shell and some crustacean appendages were found inside one of the dissected polyps, at its base. Presumably these animals were eaten, but the relatively heavy shells probably could not be expelled by the weak musculature of the zoanthid's column.

**STUDY OF PRESERVED SPECIMENS.**—Asexual reproduction seems to be predominant in *Isaurus duchassaingi* colonies because most adult individuals had pale tan gemmae sprouting from their stolons and growing obliquely from their bases. Also present among the colonies were solitary, smooth polyps, about 4 mm or more in length, which probably formed as buds and then detached from the parent. The mesenteries of many of the colonial polyps from the algal belt contained numerous large ova, about 200  $\mu\text{m}$  in diameter, and oval spermares, about 50  $\mu\text{m}$  by 100  $\mu\text{m}$  (Figure 210). Some polyps were sterile, and others had only developing ova.

All preserved polyps are in retracted postures even though they had been narcotized for several days. Polyps are yellowish white, and adult forms average 4 to 5 cm in length and 7 to 8 mm in width. A sagittal cut through a preserved retracted polyp reveals a preoral chamber below the closed capitulum, wherein lay the infolded tentacles, about 1 to 3 mm in length, usually varying in number from 38 to 42 (Figure 209a). The thick mesodermal sphincter muscle above the tentacles surrounds the top of the contracted cup-like, preoral chamber. At the base of the chamber is a slightly elevated, slit-like mouth opening, 2 to 3 mm in length, which leads to a longitudinally plicated actinopharynx, about 6 mm in length. The body wall is about 0.5 mm or more in thickness, and of greater thickness at the level of the tubercles. Most gastric filaments are brownish in color.

### Discussion

Numerous colonies of *Isaurus duchassaingi* live on the reef crest northeast of South Water Cay, Belize, and survive under austere environmental conditions. Endean (1976) described the influence

of such factors on the biota on coral reefs: mechanical damage from force of water movement, and movement of coral sand and rubble by waves; salinity changes and exposure to fresh water from rain; temperature changes; emersion of animals at low tide; changes in light intensity and degree of turbidity; predation by animals; and competitive interaction for space. Nonetheless, *I. duchassaingi* has successfully adapted to the intertidal, shallow, reef-crest zone of South Water Cay, where temperatures, salinity, sunlight, wind and wave action are extreme and variable.

*Isaurus duchassaingi* also lives in deeper water. A few colonies were seen at 10 m depth on the reef terrace, east of Carrie Bow Cay. C. Arneson (pers. comm., 1979) has seen them attached to dead coral at depths of 15 to 20 m between coral ridges in sandy areas off Mona Island, west of Puerto Rico; off Puerto Rico; and off St. Croix, Virgin Islands. The polyps, however, were not as numerous at any of these locations (only isolated groups of five to eight polyps) as those found on the reef crest of South Water Cay.

Previous observers have noted that all *Isaurus* species prefer a coral rubble or rocky substrate (McMurrich, 1889, 1896; Haddon and Shackleton, 1891; Duerden, 1898, 1902; Carlgren, 1938; Day, 1969; Walsh and Bowers, 1977). Herberts (1970, 1972a, 1972b) found that *I. spongiosus* from Madagascar occurred only in areas where variously sized coral rubble was present. Mona Island specimens have been seen nestled in rocks in 1 m of water with strong currents (R. Larson, unpublished data, 1975). *Isaurus* sp. has also been seen adhered to pieces of rock in the intertidal zone of northwest Tobago (R. Larson and K. Larson, unpublished data, 1977). The bases of Belize specimens were likewise attached to coral; the cementation of stolon and coenenchyme to parts of adjacent coral rubble enhanced stability of the animals and of substrates, and helped to retain additional sediments. Whether they adhere to shells, rocks, or pieces of coral, all known *Isaurus* species do attach to a hard substrate.

Degree of emersion is apparently a major factor determining vertical zonation of intertidal zoanthids (Herberts, 1972a). Herberts found *Isaurus*

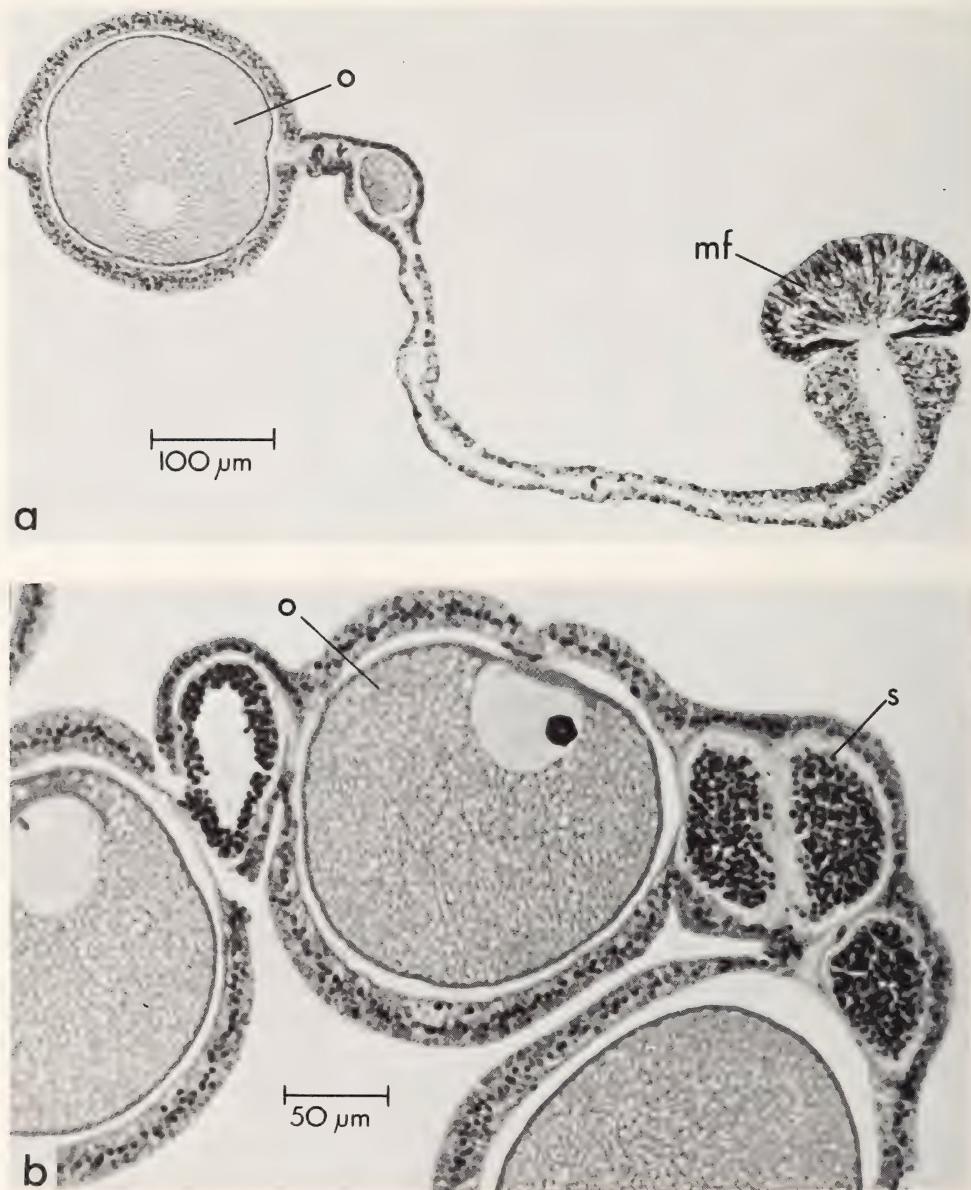


FIGURE 210.—*Isaurus duchassaingi*, transverse section across mesentery below the actinopharynx of hermaphroditic polyp: *a*, ova and mesenterial filament; *b*, ova and spermaries. (*o* = ovum, *mf* = mesenterial filament, *s* = spermary.)

*spongiosus* near midtide level, intermediate between species of *Zoanthus* and *Palythoa*. Similarly, in Belize *I. duchassaingi* was located between very shallow *Zoanthus sociatus* and deeper *Palythoa* sp. There we noticed that *Z. sociatus* tolerates a high degree of desiccation by contracting the column and closing the oral disc around the

tentacles, whereas *Palythoa* sp. probably can survive only brief periods of exposure to air. *Isaurus* species, however, withstand moderate periods of exposure, during which they are dampened by wave swash and stray water droplets from pounding waves nearby.

On the reef crest, *Isaurus duchassaingi* has

adapted to its habitat by protecting itself from desiccation and from abrasion by coral debris and potential predators. During daytime low tides, water loss from the polyps is minimized because the adults are partially buried and contracted, the capitulum is closed, and the body is near the moist substrate; the pale, smooth, thinner young polyps are never exposed, being sheltered by the adults above them. The adult polyps are also protected by a thick, tubercular column wall covered with a cuticle, sometimes with adhering unicellular algae (Duerden, 1898, 1902). Duchassaing and Michelotti (1860, 1864) noted the coriaceous tegument of *I. duchassaingi*. Herverts (1970, 1972b) remarked that her specimens had an ectodermal column thickness of 60–100  $\mu\text{m}$  and a 300–600  $\mu\text{m}$  mesogleal layer that was even thicker at the level of the tubercles; Belize specimens are similar. Furthermore, abundant nematocysts in the column ectoderm (Andres, 1877; Duerden, 1902; Carlgren, 1938; Herverts, 1970, 1972b) may deter some predators from grazing on the polyps. Thus, behavioral adaptations as well as the animal's own morphological adaptations protect the colony from desiccation and abrasion.

Although not an obvious limiting factor for distribution of *Isaurus*, light is essential for growth of symbiotic zooxanthellae. *Isaurus* species are known to have zooxanthellae in the ectoderm and endoderm of the body wall, in the endoderm of the mesenteries, as well as in the endoderm of the tentacles (McMurrich, 1889; Haddon and Shackleton, 1891; Duerden, 1898, 1902; Carlgren, 1938; Herverts, 1970, 1972b; Trench 1974), although the significance of these dinoflagellates in *Isaurus* is unknown. Sebens and DeRiener (1977) postulated that anthozoan structures adapted for photosynthesis—that is, those containing dense populations of zooxanthellae—respond positively to light (expansion, positive orientation). This is true for the exposed, sunlit—though contracted—column of *Isaurus*. Trench (1974) showed that in the zoanthid *Zoanthus sociatus*, zooxanthellae contribute substances that are utilized. Sebens and DeRiener (1977) noted the high oxygen produc-

tion of zooxanthellae. Perhaps conservation of nutrients and energy is part of the reason for expansion and contraction cycles (Sebens and DeRiener, 1977) in *Isaurus* species, but endogenous rhythms, individual physiological states of the polyps, and other external factors must also account for diurnal and nocturnal behavior patterns. For instance, after *I. duchassaingi* polyps are disturbed by light at night, why do they require many hours in the dark before reexpanding their tentacles? Obviously, light is important for zooxanthellae, which presumably benefit the zoanthids; however, the reason for tentacle retraction of *Isaurus* species during the day or in response to light at night remains undetermined.

Located in a high energy area where waves are nearly always present, *Isaurus duchassaingi* from South Water Cay is ensured of a food supply of zooplankton and larger macroscopic prey. Sebens (1976) found that *Stoichactis helianthus*, abundant on reefs in Panama wherever there was heavy wave action, ate gastropods and echinoids brought in by the waves. Likewise, *Isaurus* spp. may capture prey tossed nearby; it has tentacle spirocysts (Carlgren, 1938; Herverts, 1970, 1972b) capable of adhering to prey and has muscular tentacles capable of quickly transferring the food into its preoral chamber, which is simultaneously capped by the contracting capitulum.

Competition with other organisms for space or food may be minimal for *Isaurus duchassaingi* colonies inhabiting the reef crest of South Water Cay. Being the largest sessile organism in the algal belt, *I. duchassaingi* can overgrow the smaller organisms in its niche and can rise above them when expanding to feed at night. Motile animals (such as mollusks, echinoids, crustaceans, and fish) could enter its habitat during high tides, but this infringement would be only temporary. Although *I. duchassaingi* may be rasped by fish or other invertebrates, or jabbed by shore birds, we saw no apparent damage to the zoanthids.

Colony size and growth form of *Isaurus duchassaingi* vary. At South Water Cay, there were greater numbers of this zoanthid than have ever been reported elsewhere. The largest colony of *I.*

*duchassaingi* had more than 100 animals in adjacent groups of five to six polyps, joined either by the coenenchyme or stolon; some polyps were separate, and the smallest group had two solitary forms. Duchassaing and Michelotti (1860, pl. 8: fig. 5) originally showed four adjacent polyps on one coenenchymal base, but in their later figures, they drew two polyps united by a stolon (Duchassaing and Michelotti, 1864, pl. 6: figs. 2, 3). McMurrich (1896, pl. 17: fig. 6) reported specimens from the Bahamas as solitary, but aggregated in groups of five to six, with one specimen having a bud connected to it. Duerden reported Jamaican and Puerto Rican polyps in small clusters, or more often, solitary (Duerden, 1898, pl. 17: fig. 4; 1902, pl. 2: fig. 5). Other related species of *Isaurus* also vary in colony size and mode of growth, that is, solitary or colonial; and growing from stolons or coenenchyme (Gray, 1828; Andres, 1877; McMurrich, 1889; Haddon and Shackleton, 1891; Verrill, 1928; Carlgren, 1938; Herberts, 1970, 1972b; Day, 1969; Walsh and Bowers, 1977).

*Isaurus duchassaingi* shows a remarkable variability in dimensions of the retracted column, in color, and in size, shape and distribution of tubercles. Our adult retracted specimens have average column lengths between 4 cm and 5 cm. Bermuda, Bahama, and some Caribbean specimens have shorter columns, such as reported by Duchassaing and Michelotti (1860, 1864), McMurrich (1889, 1896), and those examined by us (British Museum (Natural History): B.M. 1901.3.8.58-60, B.M. 1927.9.9.1; American Museum of Natural History No. 691, No. 1290); many of these specimens do not exceed 3.5 cm in length. On the other hand, C. Arneson (pers. comm., 1979) has noted *I. duchassaingi* polyps as long as 12 cm. Therefore, column length of *Isaurus* may vary according to age of the polyps, habitat, and individual states of contraction when alive and during preservation.

Color of the exposed columns of *Isaurus* varies with species and location but generally blends with the surroundings. Hawaiian specimens, like the Caribbean ones, are brownish, with upper

areas of the column bright green (Verrill, 1928; Walsh and Bowers, 1977). Animals from the Indian and Pacific oceans have some additional red color on the column, particularly at the level of the tubercles (Haddon and Shackleton, 1891; Carlgren, 1938; Herberts, 1970, 1972b). Color of the exposed portion of the polyps may depend on the genetic composition of the animal, and, to a greater extent, on zooxanthellae and epizoic algae, such as the algal tufts noted by Duerden (1898, 1902). The buried lower portion of the columns of all *Isaurus* species is whitish.

Arrangement of column and crown tubercles appears to be random in all *Isaurus* species; distribution of tubercles on the concave and convex aspects of the columns varies from polyp to polyp. External morphology differs even among polyps that have grown from the same stolon. Column tubercles vary in shape from tiny verrucae to more alated protuberances, and may or may not be contiguous. For South Water Cay animals, tubercles are usually more prominent on the convex side, being situated randomly or in rows, or both, whereas the concave part has fewer, smaller tubercles or none at all; however, a preserved specimen from nearby Water Cay (B.M. 1927.9.9.1) has prominent tubercles (in rows on the convex side, scattered on the concave) completely around the column. Other Caribbean specimens may have prominent tubercles scattered all around the polyp. Crown tubercles are prominent knobs or slight bumps, or both; these tubercles are in partial or complete circular arrangement. External features of *Isaurus* may vary because of differential, endogenous rates of development, varying states of nutrition from prey or symbiotic zooxanthellae, or environmental influences.

Asexual reproduction by budding from the gastrodermal solenia of the stolon and at the coenenchymal base of adults may be the most successful means of reproduction for *Isaurus duchassaingi* on South Water Cay. Colonial forms are numerous, most of them are adjacent to each other in groups of three to eight polyps that are joined by coenenchyme or anastomotic stolons, or

both. As their basal tissue atrophies from the stolon or coenenchyme, polyps become solitary.

Little is known about sexual reproduction in zoanthids, probably because of small samples, inability to culture larval forms, or lack of seasonal data owing to short observation times. C. Arneson (pers. comm., 1979), who has observed *Isaurus duchassaingi* in aquaria for many years, has never seen them spawn. Previous authors did not mention gonads in species of *Isaurus*, except for noting female gametes in a few specimens (Duchassaing and Michelotti, 1860; Haddon and Shackleton, 1891; Herberts, 1970, 1972b). McMurrich (1889) was the only worker to find both ova and spermatozoa together in preserved *Isaurus* sp. polyps from Bermuda. Many polyps of *I. duchassaingi* from South Water Cay, Belize, are also hermaphroditic. As in McMurrich's descriptions (1889), the male and female gonads in Belizean polyps are irregularly arranged without specific positions along the mesenteries. Many Belizean polyps had only ova of various sizes, some that were possibly ready to be released; other polyps were sterile. Hence, it appears that *I. duchassaingi* from the Caribbean has monoecious and possibly also dioecious reproduction. Seasonal reproductive cycles have been reported for Zoanthidea from Okinawa and Hawaii (Yamazato et al., 1973; Cooke, 1976) and perhaps this

is also the case for species of *Isaurus*. Yamazato et al. (1973) have determined that some colonies of *Palythoa tuberculosa* Esper from Okinawa undergo sexual changes with the passage of time: female polyps change after six months to hermaphroditic polyps; after the ova are released, the testes remain and the polyps became functional males. Whether sexual changes occur in *Isaurus* remains undetermined until reproductive states of the polyps can be studied year-round.

The natural prey of *Isaurus* is unknown. Since *I. duchassaingi* expands its tentacles to feed only at night, it is a nocturnal carnivore. In the laboratory, *I. duchassaingi* preferred larval fish, and did not capture small crustaceans readily, except for *Artemia salina* nauplii. On the reef crest, however, *I. duchassaingi* may select larger organisms in the zooplankton as food because the zoanthid has a widened preoral chamber, which is rimmed by nematocyst-laden tentacles. Furthermore, the zoanthid has strong sphincter muscles that close the capitulum simultaneously with the introversion of the tentacles, thus facilitating swift containment of the prey. C. Arneson (pers. comm., 1979) has kept *I. duchassaingi* from Puerto Rico in good condition in aquaria for over three years without feeding them. The importance of prey and zooxanthellae for the nutritional requirements of these zoanthids is unstudied.

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# Larval Settlement Behavior and Shell Morphology of *Malleus candeanus* (d'Orbigny) (Mollusca: Bivalvia)

Thomas R. Waller  
and Ian G. Macintyre

## ABSTRACT

Data on larval settlement behavior and shell morphology of the little known bivalve, *Malleus (Malvufundus) candeanus* (d'Orbigny, 1842), were obtained from an experiment designed for obtaining data on the distribution of boring microorganisms. Plastic (PVC) tubes with screened ends enclosing crushed coral fragments were set out on a transect line crossing the reef at Carrie Bow Cay, Belize. Epifaunal bivalves, half of which proved to be members of this species, attached to the containers during the 10-month sampling period. The distribution of specimens of *M. candeanus* among opaque versus transparent tubes and the positions of attachment sites on the walls of containers suggest that their planktonic larvae are both photonegative and geonegative at time of settlement. In nature the larvae probably swim to a dark area beneath an overhang and then move laterally to the intersection of two surfaces, such as the bottom of a crevice, where they attach with a byssus and then metamorphose.

*Malleus candeanus* trapped in the tubular containers approached full adult size in less than 10 months. Unlike naturally occurring specimens they have a more regular shell outline and better developed posterior auricles and lack a central constriction and distal flare in the posteroventral prismatic extension of the shell. Therefore, the lack of a posterior auricle and presence of an irregular shell outline are probably phenotypic

characteristics that cannot be relied on in taxonomic studies.

## Introduction

*Malleus (Malvufundus) candeanus* has received little attention in the literature on western Atlantic Mollusca since its original description by d'Orbigny (1842) as *Avicula candiana* (type-locality, Santiago de Cuba, in a large sponge). Johnson (1918) reported the presence of the species in Bermuda and briefly discussed its taxonomy. The only other detailed treatment is that of Boss and Moore (1967), who established that the species is broadly distributed, though "rarely encountered," in Bermuda, the tropical western Atlantic, and the tropical eastern Pacific. More recently, however, Waller (1973 and unpublished data) and Abbott (1974) found that the species is common among corals in Bermuda, the east coast of Florida, and in Belize, and Rosewater (1975 and unpublished data) found it to be common among rocks at Ascension Island in the South Atlantic. Specimens are seldom encountered not because they are rare, but because their cryptic living habit and irregular, fragile shell make them difficult to find and collect.

The present study is concerned with specimens of this species found byssally attached in cylindrical plastic containers with screened ends that were placed on a transect line crossing the reef at

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Carrie Bow Cay, Belize. The distribution of these specimens among opaque and transparent containers and their preferred living positions yield information on the settling behavior of larvae; the size of the shells gives an estimate of minimum growth rate; and the shapes of the post-larval shells provide insight into the relationship between shell form and living habit. Comparison of specimens from the containers with those from natural habitats in the same area suggests that some features previously considered important in the taxonomy of *Malleus* are phenotypic responses to living conditions.

**MORPHOLOGY AND SYSTEMATICS.**—Like other members of the Order Pterioida (emend. Waller, 1978), *Malleus (Malvufundus) candeanus* has a shell composed of an inner layer of nacreous aragonite and an outer layer of simple prismatic calcite (Taylor et al., 1969). As in the closely related species *Malleus (Malvufundus) regulus* (Forskål), the anatomy and habits of which have been described by Yonge (1968), nacreous aragonite is limited to the dorsal one-fourth of the shell and prismatic calcite forms a long extension of the shell margin in a posteroventral direction. The visceral-pedal mass occupies the nacreous dorsal region, whereas only the mantle and ctenidia lie in the prismatic extension.

Several subgeneric names based primarily on the presence or absence of anterior and posterior extensions of the hinge have been introduced for groups within the genus *Malleus*. Boss and Moore (1967) questioned the taxonomic reliability of hinge extensions except in two groups: one having both anterior and posterior hinge extensions [*Malleus (Malleus)* Lamarck, the "hammer oyster"]; the other having "hardly any lateral extension of hinge line" and designated *Malleus (Parimalleus)* Iredale. Hertlein and Cox (1969) and Keen (1971) used the prior subgeneric name *Malvufundus* De Gregorio for the second group, thereby suggesting that minor differences in poorly developed hinge extensions originally used to separate *Parimalleus* and *Malvufundus* are insignificant for the distinction of subgenera. Variations in the development of a posterior auricle in

*M. candeanus* are well documented: d'Orbigny (1842) showed a distinct posterior auricle; Johnson (1918) showed only a slight irregular posterior extension of the dorsal region; and Boss and Moore (1967) showed none.

Many species names have been introduced for populations of the subgenus *Malvufundus* that occur in the tropical and warm-temperate regions of the world oceans. All exhibit a highly irregular shell form and tend to settle on hard substrates in crevices or beneath overhanging ledges. A taxonomic review of these nominal taxa has not yet appeared, and there is no agreement on the number of valid species. Boss and Moore (1967:87) have summed up the problem of relationships concisely: "The major problem with *Malvufundus* is whether or not there is only a single extremely variable species in the Mediterranean-Indo-Pacific region [*Malleus regulus*], and if so, whether that species can be truly differentiated from *M. candeanus*."

In distinguishing the New World *Malleus candeanus* from the Mediterranean-Indo-Pacific species complex, Boss and Moore (1967) considered three regions of the shell: (1) a dorsal part frilled on the exterior by broad, overlapping sheets of prismatic calcite, some of which may fuse to form large, enclosed voids; (2) a central, narrow region—the "shank"—which is not strongly frilled on the exterior and is buttressed by a single rib on the inner shell surface; and (3) a flared, "fan-shaped" ventral area. They suggested that this tripartite division of the shell is more distinct in *M. candeanus* than in other species of the subgenus *Malvufundus*.

**ECOLOGY.**—In the vicinity of Carrie Bow Cay, Belize, specimens of *Malleus candeanus* are common from a depth of 5 m in the high-relief spur and groove zone seaward to the deepest area explored by SCUBA diving, 46 m on the steeply inclined fore-reef slope (Figure 211). Specimens are less common in shallower water. In the wave-washed *Millepora complanata* Lamarck of the reef-crest zone and in the lagoon landward of Carrie Bow Cay, *Malleus* is uncommon and is replaced by *Isognomon radiatus* (Anton), which is very similar morpholog-

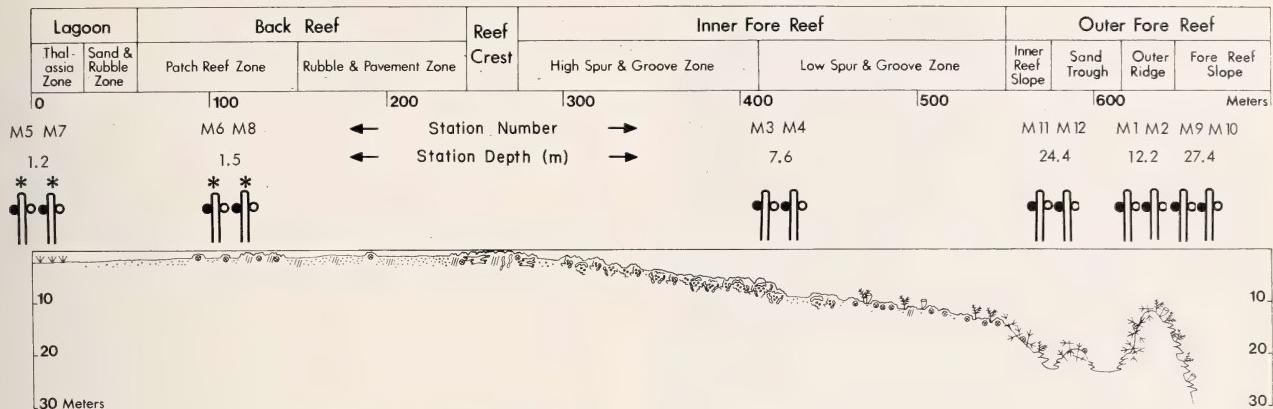


FIGURE 211.—Profile of reef at Carrie Bow Cay, Belize, showing location of stations, each station consisting of two containers, one opaque and the other transparent (asterisks indicate algal-covered and damaged containers that yielded no specimens).

ically and ecologically, living in holes and crevices and beneath overhanging ledges. Although morphologically similar species of *Isognomon* and *Malleus* (*Malvulfundus*) may co-occur in abundance in some regions of the Pacific Ocean (Yonge, 1968), this is not the case in Belize.

Individuals of *Malleus candeanus* commonly live on the downward facing surfaces of overhanging ledges. The shells are attached by a strong byssus, with the dorsal or right anterodorsal region of the shell against the attachment surface and the posteroventral extension hanging downward. Specimens were common at the inner limits of overhangs, less common on vertical walls. In only one case were young specimens found on an upward facing surface; one individual was hanging downward inside a dead, articulated, nearly closed shell of *Spondylus*. As noted by Boss and Moore (1967), Waller (1973), and in the present study, specimens do not ordinarily live in sponges, the type description notwithstanding. Quantitative data on population density are lacking, but our observations during diving suggest that *Malleus candeanus* is not unusually abundant in the area of the reef transect.

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## Materials and Methods

Twelve pairs of sediment containers holding crushed coral fragments were placed at intervals along a transect line crossing the reef at Carrie Bow Cay, Belize, by Macintyre for the purpose of gathering information on distribution of boring microorganisms (unpublished). Each container was a cylinder of either opaque gray or transparent colorless plastic PVC (polyvinyl chloride) pipe 65 mm in length and 50 mm in diameter and each had gray, plastic-coated fiberglass screening (mesh size about 1 mm) fastened with epoxy resin over each end. The containers were positioned in pairs, one opaque and one transparent, at each station in the manner shown in Figure 212. Distance from the containers to the bottom was approximately 50 cm. Distribution of stations along the transect line is shown in a profile (Figure 211), and the location of the transect is shown by Rützler and Macintyre (herein, Figure 4). The containers were set out between 7 June and 13 June 1972 and were collected between 5 April and 11 April 1973, approximately 10 months later.



FIGURE 212.—Substrate station M6 in the patch reef zone. Browsing fish have destroyed the screened ends of the cylindrical sediment containers.

The containers were placed in neutral buffered formalin at the time of collection. Because it was not apparent until they were emptied at a later time that they contained *Malleus*, no on-site data on the final orientation of the cylinders or of the exact living positions of bivalves in them were taken. The top and bottom of the containers, however, could be inferred later from the distribution of encrusting organisms, the top surface generally being covered with algae and the bottom having sparsely distributed worm tubes. The attachment sites of *Malleus* on the interiors of several of the cylinders could be determined by examination with a binocular microscope, because the byssus was left attached to the wall of the container when specimens were removed.

The dorsal region of the shell of one small specimen from station M11 (USNM 782900, Figure 213) was washed in neutral distilled water, sputter coated with carbon and then gold palladium to a thickness not exceeding 7.5 nm, and examined in a Coates and Welter 106B scanning electron microscope.

## Results and Discussion

Containers shoreward of the low-relief spur and groove zone on the transect (stations M5-M8, Figure 211) were covered with algae and their screens were destroyed by browsing animals. Because they contained no specimens of *Malleus* or of any other epifaunal bivalves on either their outer or inner surfaces, they will not be considered further.

In contrast, the eight pairs of containers seaward of the high-relief spur and groove zone remained intact (with the exception noted below) and contained an assemblage of five species of living epifaunal bivalves at the time of collection. The distribution of these specimens with respect to the inside and outside of opaque and transparent containers at each station is given in Table 42. Thirteen of the 27 individuals tabulated are *Malleus candeanus*, a surprising result in view of the fact that there does not seem to be an unusually dense population of the species in this area.

A striking difference in settlement behavior among the five species of bivalves can be seen in Table 42. Of the 13 specimens of *Malleus candeanus*, nine attached to the inner walls of the cylinders. Only one individual of the 14 specimens of other species was found inside a cylinder; all of the other specimens were on outer walls or on outer sides of screens. Furthermore, all of the specimens of *M. candeanus* found on inner walls were in opaque containers. In contrast, individuals of all species attached to outer walls were about evenly divided between opaque and transparent containers.

The veliger larvae of *Pinctada*, *Spondylus*, and *Chama* are known to be planktonic (Martinez-Escarbassiere, 1970; Kennedy et al., 1970; La-Barbera and Chanley, 1971; Rosewater, 1975; Waller, unpublished data), lifting themselves off the bottom by the action of a ciliated velum. Larvae of *Lopha*, after an initial brooded stage (Stenzel, 1971), are also planktonic. Although living larvae of *Malleus candeanus* have never been observed, their small prodissococonch-I stage (now known to represent the initial phase of larval

TABLE 42.—Epifaunal bivalves in or on cylindrical containers at Carrie Bow Cay, Belize  
(stations listed landward to seaward for each species)

Species	Station	Number of specimens				Maximum dimension of measured specimen(s) (mm)	
		Opaque containers		Transparent containers			
		Inside	Outside	Inside	Outside		
<i>Malleus candeanus</i> (d'Orbigny)	M3	0	0	0	1	12	
	M4	1	2	0	0	37	
	M11	3	1	0	0	24	
	M12	1	0	0	0	41	
	M1	1	0	0	0	(broken)	
	M2	2	0	0	0	40	
	M10	1	0	0	0	(broken)	
<i>Pinctada imbricata</i> Röding	M3	0	0	0	2	14	
<i>Spondylus</i> sp.	M9	0	1	0	0	5.5	
<i>Lopha frons</i> (Linnaeus)	M3	0	2	0	1	16	
	M4	1	0	0	0	13	
	M12	0	2	0	0	5.6	
	M10	0	0	0	2	28	
	M11	0	0	0	1	5	
<i>Chama</i> sp.	M9	0	0	0	2	5	

growth before the valves of the larval shell can enclose the body) and relatively large prodissoconch-II stage (Figure 213) indicate a planktonic, planktotrophic mode of life (Ockelmann, 1965; Waller, 1981). A planktonic mode of life is also indicated by the fact that the larvae entered containers 50 cm off the bottom.

The fact that all of the specimens of *M. candeanus* occurring on inner walls were in opaque containers cannot readily be explained except in terms of larval behavior during the swimming and crawling stage just prior to and at the time of settlement. The sizes of prodissoconchs (larval shells) of all species found on and in containers (Table 43) are well below the 1 mm mesh size of the screens. Despite the reduction in size of mesh openings caused by algal encrustations, these openings were still adequate to allow penetration of bivalve larvae. It thus appears that larvae of *M. candeanus* are distinctly photonegative at the time of settlement and that they have a greater ability to select and enter dark, obstructed spaces than other larvae present during the sampling period.

Additional information on the settling behavior of *Malleus candeanus* can be obtained from the attachment sites on container walls. Three byssal attachments found on the inside walls were at or near the top adjacent to a plug of epoxy resin, which was holding the rope that fixed the container to the pole (Figure 212). Attachment sites on the outside walls were either at the bottom, between the tube wall and the folded-back edge of the screen, or (in one case) in a downward opening crevice formed between an attached oyster and the wall of the container. The larvae of *M. candeanus* thus appear to be geonegative as well as photonegative at the time of settlement. They probably swim upward until they contact a suitable overhang and then move laterally until they perceive a crevice or an intersection of two surfaces.

The sizes of the shells of trapped specimens of *Malleus candeanus* give a rough indication of growth rate. With the exception of one individual (station M1), all specimens in the cylinders were living and presumably actively growing at the time of collection. The only dead specimen, which

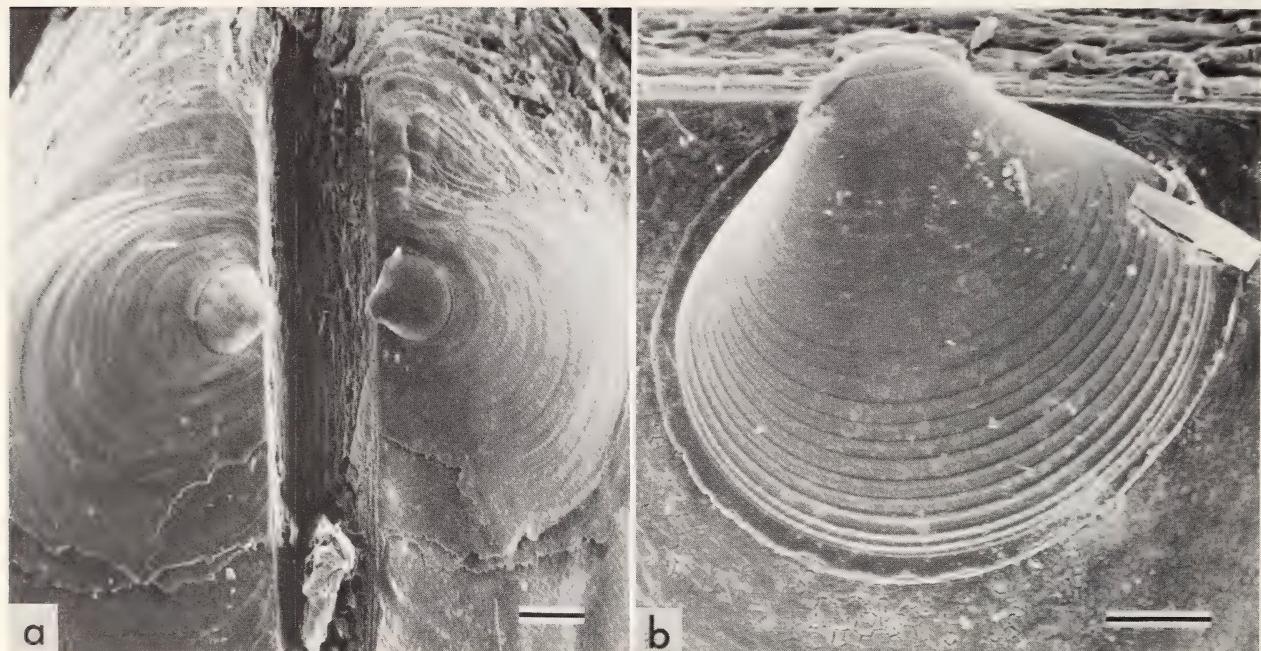


FIGURE 213.—Prodissococonch of *Malleus (Malvafundus) candeanus* from station M11, USNM 782900: *a*, dorsal view of dorsal region, anterior toward top,  $\times 43$ , scale bar = 200  $\mu\text{m}$ ; *b*, detail of right valve of prodissococonch showing small prodissococonch-I stage (top) and relatively large, commarginally ridged prodissococonch-II stage,  $\times 280$ , scale bar = 50  $\mu\text{m}$ .

TABLE 43.—Prodissococonch size of specimens on or in containers at Carrie Bow Cay, Belize

Species	Number of specimens measured	Length of prodissococonch ( $\mu\text{m}$ )		
		Min.	Max.	Mean
<i>Malleus candeaus</i> (d'Orbigny)	13	265	326	288
<i>Pinctada imbricata</i> Röding	1	—	—	306
<i>Spondylus</i> sp.	1	—	—	194
<i>Lopha frons</i> (Linnaeus)	4	398	428	416
<i>Chama</i> sp.	1	—	—	184

had a circular hole with beveled edge on its left valve, was killed by a predatory gastropod that entered the container through a large hole in one of the screens. Measuring from beak to the margin of the posteroventral prismatic extension of the shell, we observed a maximum size of 56 mm in shells of this species in the Division of Mollusks,

National Museum of Natural History (USNM 457011, Southwest Channel, Tortugas, Florida, depth 18 m). The largest trapped individual (40 mm, station M12) had attained 73 percent of the size of the largest museum specimen and must have been approaching maturity. If it be assumed that the larva of the 40 mm specimen entered the container at the beginning of the 10-month sampling period, its growth rate would be 4 mm per month. This represents a minimum estimate; if the larva entered later, the calculated growth rate would be higher.

The shells of specimens removed from the containers differ from those of specimens living under natural conditions in that they have a posterior auricle and lack a central "shank" and distal flare (Figure 214). Both differences appear to result from the unusual environment in which larvae settled. Compared to natural settlement surfaces, the walls of the plastic tubes were relatively free of epifauna and presented a smooth surface for attachment. Subsequent growth away from the



FIGURE 214.—*Malleus (Malvufundus) candeanus*: a, right side of specimen from inside container at Station M4, USNM 782901; b, right side of specimen from natural habitat on Carrie Bow Cay reef at depth of 9 m, USNM 782902; c, left side of specimen from inside container at Station M12, USNM 782903; all  $\times 2$ , lightly coated with ammonium chloride.

surface was into a protected and, in view of the small maximum size of this species, unconfined space.

The development of a posterior auricle is apparently hindered in naturally occurring specimens because dorsal shell expansion is confined to a narrow or irregular space. Among museum specimens, a posterior auricle is absent from specimens of *Malleus candeanus* and closely related or conspecific Pacific taxa collected from reefs,

where they presumably lived in holes and crevices. In contrast, a posterior auricle is present in many specimens of *M. (Malvufundus) regulus*, which appears to occur on bare rock surfaces more commonly than in holes and crevices (Yonge, 1968). Extreme development of a posterior auricle and an anterior auricle-like extension of the dorsal margin occurs in *M. (Malleus)*, the "hammer oyster." Yonge (1968:387), in referring to *M. malleus*, said that the shell "is always buried

with only the distal quarter or less exposed" and that "the extent of exposure is usually revealed by the presence of encrusting organisms absent from buried regions of the shell." In specimens of this species in the collections of the National Museum of Natural History both valves are entirely encrusted with organisms that were alive at the time of collection, and thus we infer that these specimens cannot have been buried in the manner assumed by Yonge to be typical. They more likely were attached to rocky surfaces or to rubble on the bottom, as reported by Chuang (1961) and R. T. Abbott (pers. comm.).

These differences between specimens living under natural conditions and those living in artificial, protected, unconfined spaces support suppositions that minor differences in hinge extension are unimportant for the distinction of subgenera. They further suggest that minor differences in shell outline, such as the central constriction and distal flare of the prismatic region thought by Boss and Moore (1967) to be useful in distin-

guishing *M. candeatus* from congeneric species, may also be unreliable.

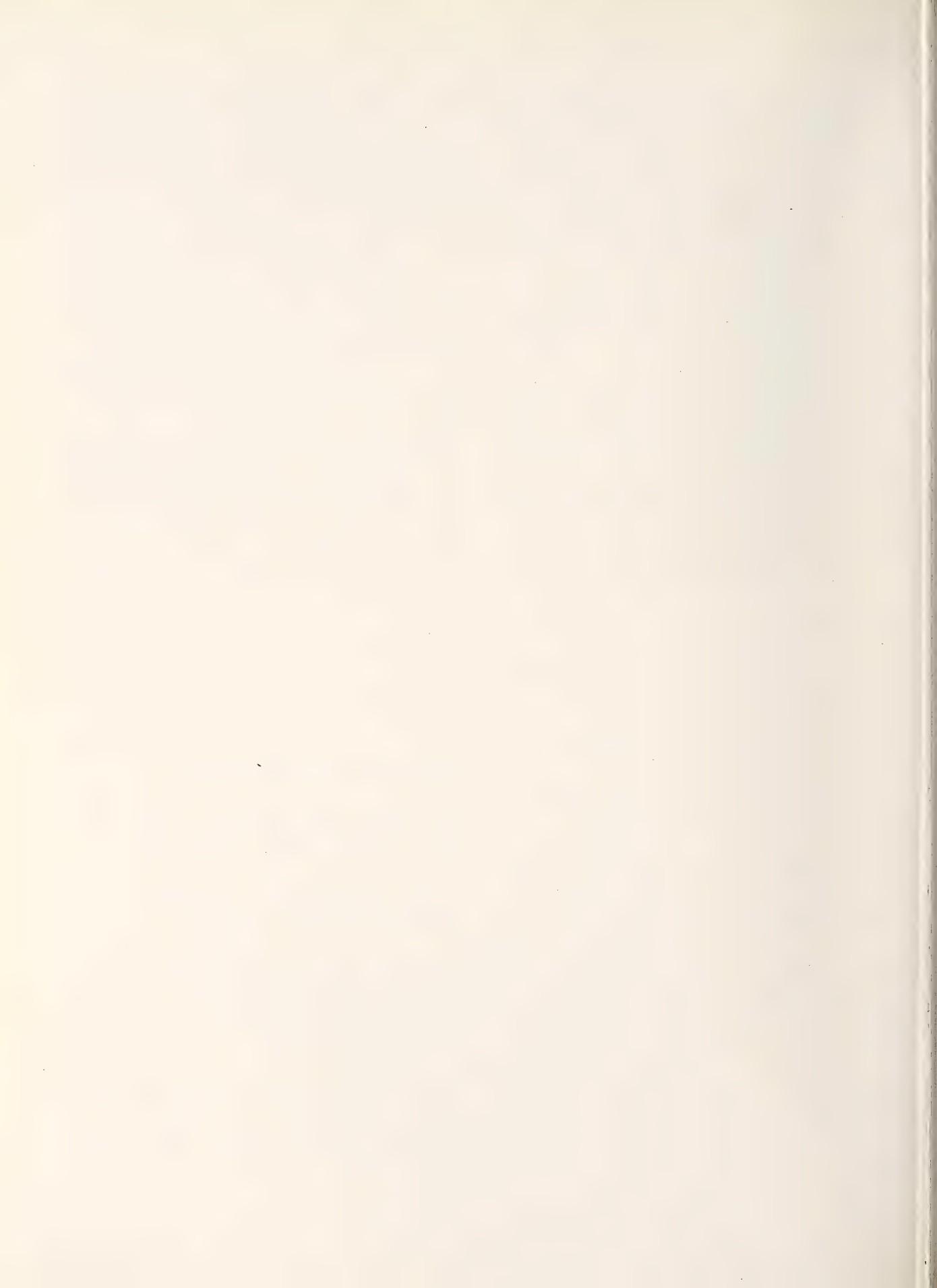
## Conclusions

The planktonic planktotrophic veliger larvae of *Malleus (Malvufundus) candeatus* respond negatively to light and gravity at the time of settlement. These responses allow them to seek out dark crevices and holes beneath overhanging ledges for byssal attachment and subsequent growth. *M. candeatus* can attain a maximum dimension of about 40 mm, which is about three-fourths of its maximum known size, within a period of time not exceeding 10 months and possibly considerably less. The degree of development of a posterior auricle, a central constriction, and a distal flared portion of the shell are all phenotypic responses to the nature of the attachment surface and are therefore not reliable subgeneric and specific differentia.

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# Habitat and Resource Partitioning between Two Species of *Acanthemblemaria* (Pisces: Chaenopsidae), with Comments on the Chaos Hypothesis

David W. Greenfield  
and Teresa A. Greenfield

## ABSTRACT

Four of the eight western Atlantic species of the chaenopsid fish genus *Acanthemblemaria* occur in Belize, Central America. At Carrie Bow Cay on the barrier reef two inquiline species, *A. spinosa* and *A. greenfieldi*, exhibit subtle habitat separation: *A. spinosa* occurs only in holes left by invertebrates on vertical surfaces of dead coral, and *A. greenfieldi* occurs only in holes left by invertebrates on horizontal surfaces of dead coral. Consequently, *A. spinosa* individuals are found primarily just behind the reef crest, whereas *A. greenfieldi* individuals are most abundant in the back reef, although both species can be found on the same coral head. A total of 168 specimens of *A. greenfieldi* and 90 specimens of *A. spinosa* was collected and analyzed for length-frequency, stomach contents, and fecundity.

Length-frequency analysis showed that *Acanthemblemaria greenfieldi* is larger than *A. spinosa* and that in both species males are larger and more numerous than females. Stomach content analysis revealed different preferential feeding of each species among the same groups of invertebrates. Fecundity analysis confirmed that females of *A. spinosa* mature at a smaller size than those of *A. greenfieldi*. Smaller females (including most *A. spinosa* females) have fewer and smaller eggs than

larger females (including many *A. greenfieldi* females). The fine habitat partitioning exhibited by these and other coral-reef fishes suggests that the chaos hypothesis of habitat selection may only apply to larger species.

## Introduction

The chaenopsid fish genus *Acanthemblemaria* is represented by eight species in the western Atlantic Ocean (Smith-Vaniz and Palacio, 1974). Four of these eight species occur in Belize, Central America: *A. aspera* (Longley), *A. greenfieldi* Smith-Vaniz and Palacio, *A. maria* Böhlke, and *A. spinosa* Metzelaar; all except *A. maria* have been taken on the barrier reef at Carrie Bow Cay, (Greenfield and Johnson, 1981).

At Carrie Bow Cay, *Acanthemblemaria aspera* has been taken only at a depth of 9 m in the low-relief spur and groove zone of the inner fore reef; however, both *A. spinosa* and *A. greenfieldi* occur in shallow areas on the reef crest and across the back reef. Both of these species are inquiline, dwelling in holes left by worms or other boring invertebrates (Figure 215). The present study was prompted by our observation of subtle differences in habitats during a faunal survey at Carrie Bow Cay.

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FIGURE 215.—*Acanthemblemaria greenfieldi* in natural habitat.

government of Belize, and especially to G. W. Miller, Fisheries Administrator, for granting permission to collect fish specimens. P. Illg, University of Washington, kindly helped to identify food items and C. F. Rakocinski, Northern Illinois University, assisted in the field. J. Glaser, Northern Illinois University, prepared the graphs. H. Bowman, Jr., was of considerable assistance in arranging field logistics. This research was supported in part by National Science Foundation Grant BMS75-08684 to D. W. Greenfield.

### Materials and Methods

Specimens were collected individually by squirting into their holes a mixture of quinaldine and isopropanol, which caused them to leave their holes. After the anesthetic effect of the quinaldine took effect, individuals were picked up by hand and placed into plastic bags labeled with detailed information on habitats. Six collections were made during the period 10–17 May 1977 and three collections during 1–4 January 1978. A

total of 168 specimens of *Acanthemblemaria greenfieldi* and 90 specimens of *A. spinosa* was taken.

Lengths, which are given as the standard length (SL) in mm, were made to the nearest 0.1 mm using dial calipers. Twenty specimens each of *A. greenfieldi* (24.3–33.8 mm SL) and *A. spinosa* (19.8–26.4 mm SL) were analyzed for stomach contents: eight individuals of each species were taken at 0930 h on 16 May 1977 and 12 of each species at 1500 h on 15 May 1977, and the data combined. Food items were sorted by taxa, counted, and their volume determined using a squash technique modified from Hellawell and Abel (1971) by Ross (1974:8, 1977:561). Relative importance of each food category was evaluated using the percentage of occurrence of food items in stomachs, the number of food items in each category, and the volumetric contribution of each prey category to total stomach volume. The relative importance of each food category was determined by the index of relative importance (IRI) (Pinkas 1971:9):  $F(N+V) = IRI$ , where  $N$  = numerical percentage,  $V$  = volumetric percentage, and  $F$  = frequency of occurrence percentage. The degree of food overlap between the two species of *Acanthemblemaria* was measured using the overlap coefficient of Horn (1966:420):

$$C\lambda = \frac{2 \sum_{i=1}^s X_i Y_i}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2}$$

$C\lambda$  varies from 0 (when two species have no food category in common) to 1 (when the proportions of each food category are identical);  $s$  = total number of food categories;  $X_i$  is the proportion of the total diet of species  $X$  for food category  $i$ ;  $Y_i$  is the similar proportion of the total diet of species  $Y$ .

Eggs were counted and measured from 36 *Acanthemblemaria greenfieldi* females (18 in January; 18 in May) and from 22 *A. spinosa* females (12 in January; 10 in May) with the aid of a dissecting microscope fitted with an ocular micrometer. Eggs were categorized by size class (ovum diameter) into separate broods:  $\leq 0.10$  mm, 0.11–0.20 mm, 0.21–0.30 mm, 0.31–0.50 mm, 0.51–0.75

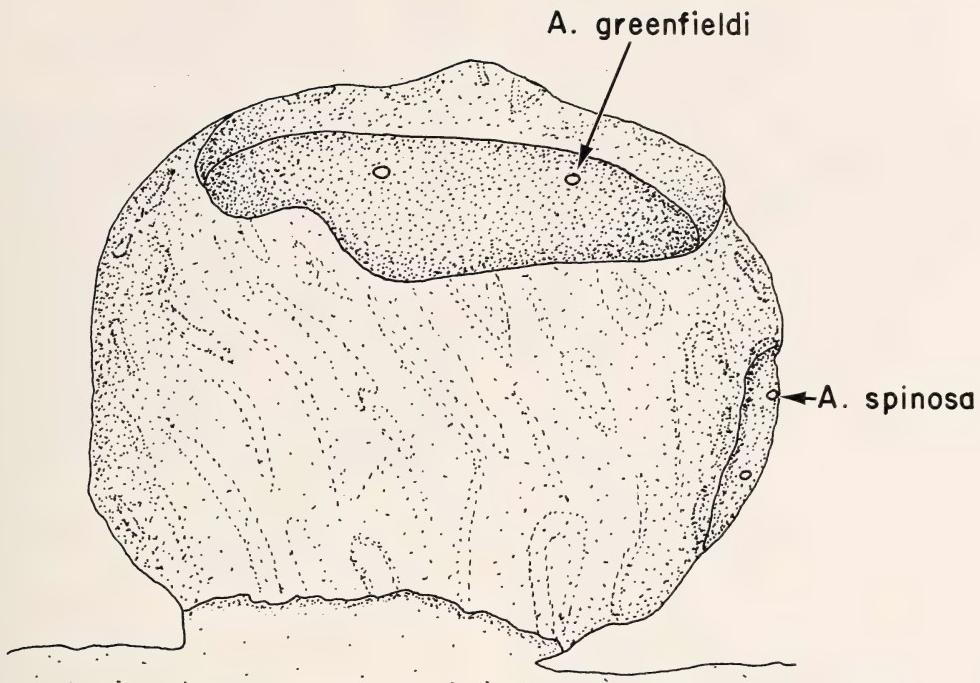


FIGURE 216.—Relative positions of *Acanthemblemaria greenfieldi* and *A. spinosa* on a single brain coral.

mm, 0.76–1.00 mm. Individual broods contained from two to 28 eggs, and individual females contained from two to three broods. Average brood size was determined by averaging the number of eggs in all broods for all females of each individual standard-length measurement.

### Results

*Acanthemblemaria spinosa* occurs only in holes left by invertebrates on vertical surfaces of dead coral. This vertical habitat is present in three distinct situations: dead basal portions of living trees of *Acropora palmata* (Lamarck), vertical surfaces of fallen dead trees of *A. palmata*, and less commonly on vertical surfaces of other corals. The restriction of this species to vertical surfaces results in an uneven horizontal distribution across the reef, with most individuals being found just behind the reef crest and in reduced numbers in the back reef.

*Acanthemblemaria greenfieldi* occurs only in holes left by invertebrates on the horizontal surfaces of

dead coral. As a result, this species is most abundant in the back reef, which is composed of coral rubble and pavement. Less commonly, this species occurs closer to the reef crest on the horizontal surfaces of fallen dead trees of *Acropora palmata*.

On 15 May 1977, 44 specimens of *Acanthemblemaria* were collected without regard to species identification. They were placed into plastic bags labeled "horizontal" or "vertical" depending on the location of capture. When the collection was subsequently examined it was apparent that 20 *A. greenfieldi* had been taken from the horizontal surfaces and 24 specimens of *A. spinosa* from the vertical surfaces. A single brain coral, *Diploria* sp., 65 cm high and 60 cm in diameter, located on the rubble and pavement zone of the back reef, provided a striking example of the sharpness of the habitat separation between these two species. The top of the brain coral, which was dead and covered by sediment, provided a horizontal surface. A small dead portion on the side of the coral head also provided suitable vertical habitat. Specimens of *A. greenfieldi* were living on the top of the

coral head, whereas *A. spinosa* was living on the side (Figure 216). Additional collections made for the feeding and life history studies have also demonstrated this separation.

On 4 January 1978, a collection was made in the coral rubble and pavement zone of the back reef just south of Carrie Bow Cay to obtain specimens of *Acanthemblemaria greenfieldi* for life history information. This location was chosen because it is a typical *A. greenfieldi* habitat and samples taken in May 1977 had contained only members of this species. Examination of the new series of 53 specimens, however, showed that it included not only 36 *A. greenfieldi* (7.6–30.3 mm SL;  $\bar{x} = 24.5$  mm SL), but also 17 young *A. spinosa* (13.4–18.4 mm SL;  $\bar{x} = 15.7$  mm SL).

Length-frequency analysis (Figure 217) shows that *Acanthemblemaria greenfieldi* is a larger species than *A. spinosa* and that males of both species are larger than females: *A. greenfieldi* males attain a length of at least 32.5 mm SL ( $\bar{x} = 25.5$  mm) and females reach 30.0 mm SL ( $\bar{x} = 23.5$  mm), whereas *A. spinosa* males attain a length of 26.4 mm SL ( $\bar{x} = 19.9$  mm) and females reach 23.2 mm SL ( $\bar{x} = 18.4$  mm). Males of both species also outnumbered females in our collections; males constituted 61% (January) and 64% (May) of the total *A. greenfieldi* sample, and 60% (January) and 65% (May) of the total *A. spinosa* sample. Within each species, the proportions of individuals within each size range were basically similar for both January and May, with the majority of *A. greenfieldi* individuals falling between 20 and 30 mm SL and the majority of *A. spinosa* individuals falling between 15 and 25 mm SL for both months.

A fecundity analysis (Figure 218) revealed that *Acanthemblemaria spinosa* females mature at a smaller size (12.4 mm SL) than do *A. greenfieldi* females (19.0 mm SL), as might be expected on the basis of the smaller overall size range of *A. spinosa*. Females of both species contained from two to three broods, or size classes of eggs. Predictably, the largest females (*A. greenfieldi*) had more eggs than the smallest females (*A. spinosa*). In addition, the largest eggs of the largest *A. greenfieldi* females averaged 0.76–1.00 mm in di-

ameter, whereas the largest ones of the smaller females, including *A. spinosa*, averaged 0.51–0.75 mm in diameter.

An analysis of the food habits of these two species during the month of May has shown that although they may feed on the same groups of invertebrates, the dependence on, or preference for, specific taxa differs considerably. The overlap coefficient yields a value of 0.4, indicating a major separation. The index of relative importance shows that both species depend heavily on copepods; however, the next item of importance for *Acanthemblemaria spinosa* is isopods, whereas isopods are only the fourth most important food

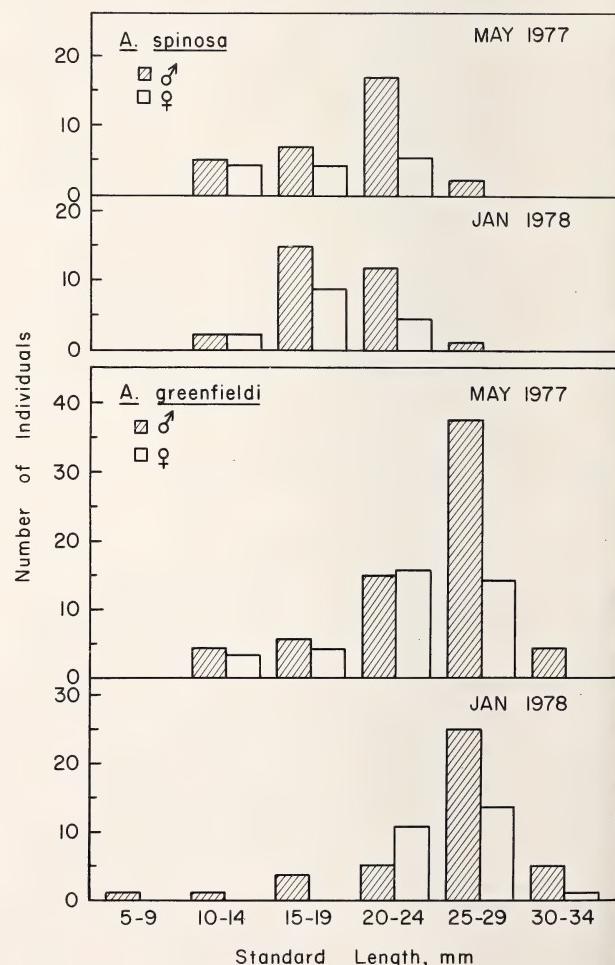


FIGURE 217.—Length frequencies of *Acanthemblemaria spinosa* and *A. greenfieldi* males and females from Carrie Bow Cay, May 1977 and January 1978.

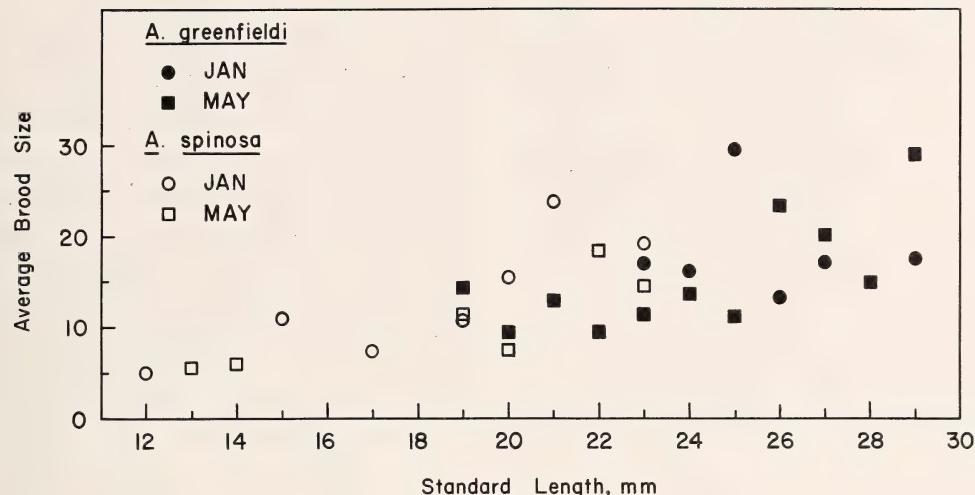


FIGURE 218.—Average brood size vs. SL of females of *Acanthemblemaria greenfieldi* and *A. spinosa* from Carrie Bow Cay, May 1977 and January 1978.

category for *A. greenfieldi* (Figure 219), which depends more on ostracods and tanaids (Figure 220).

### Discussion and Conclusions

*Acanthemblemaria spinosa* and *A. greenfieldi* exhibit extremely fine habitat partitioning; they achieve 100% separation as adults by using holes made by invertebrates on vertical or horizontal surfaces. The relatively low level of food overlap between these two species ( $C\lambda = 0.4$ ) is also probably the result of their habitat separation. Both species feed by two methods, either by extending partially out of their holes and taking food items from the substrate near the hole, or by darting out and taking plankters. The plankters taken by our specimens were mainly harpacticoid copepods, a group usually associated with the substratum. Food organisms of second importance were isopods for *A. spinosa* and ostracods for *A. greenfieldi*. The vertical dead coral surfaces where *A. spinosa* is found tend to be covered with filamentous algae that provide a typical substrate for isopods. The horizontal surfaces where *A. greenfieldi* occurs are generally exposed to sedimentation so that sand surrounds the holes in the coral, providing suitable ostracod habitat.

The 4 January 1978 collection from a typical *Acanthemblemaria greenfieldi* habitat, which also yielded young of *A. spinosa*, provides valuable information concerning the interactions of these two species. Although the adults exhibit complete habitat separation, apparently planktonic larval *Acanthemblemaria* species settle and occupy any available hole or crevice. Because individuals of *A. spinosa* found here were only 18.4 mm or less, it may be assumed that when they outgrow their holes and search for a larger hole, they are excluded by *A. greenfieldi* from this habitat. Stephens et al. (1970:228) have described similar shifts in holes with growth for the California blenny *Hypsoblennius jenkinsi*. Because *A. greenfieldi* is a larger species, it might have an advantage in holding a hole.

The horizontal habitat of *Acanthemblemaria greenfieldi* compared to that of *A. spinosa* is generally in areas of lower wave and surge action. Collecting *A. spinosa* just behind the reef crest is difficult because of the strong surge that tends to sweep the diver back and forth, whereas collecting *A. greenfieldi* does not present this problem. If the force of the water behind the reef crest poses a problem for a diver, it is logical to assume that it would be an equal or greater problem for *A. spinosa* when it darts out to obtain a food item. It

may be that the horizontal habitat available in the back reef is more advantageous for *Acanthemblemaria*, but that *A. spinosa* is excluded from the superior habitat by *A. greenfieldi*.

The fine partitioning of habitat by these two species of *Acanthemblemaria* is particularly interesting in light of Sale's (1977) views concerning habitat partitioning by coral-reef fishes. Sale concluded (1977:341): "We do not find, as a general rule, a high degree of specialization on microhabitats and a resulting fine partitioning of living space." He also noted that "there are a minority of species on reefs with highly specialized habitat needs, especially among fish with inquiline habits;" however, "the habitat requirements of coexisting habitat specialists often overlap greatly." Sale listed four examples from the literature of sponge-dwelling gobies, coral-dwelling

gobies, and anemone fishes where two or more species were collected in the same sponge, coral or anemone. Until more detailed studies have been conducted, however, a single organism, such as a sponge, should not necessarily be considered to provide a single habitat. Position of fishes within the sponges must first be investigated, for it is certainly possible that one species may be restricted to the opening and another to the inner part of the sponge atrium.

The chaenopsid blennies found in Belize provide an example of a group of fishes that have finely partitioned the habitat. The two species of *Acanthemblemaria* investigated in this study demonstrate that a single, small brain coral cannot be considered a single habitat because habitat partitioning was effected by distinguishing between horizontal and vertical surfaces. Other chaenopsid species provide additional examples.

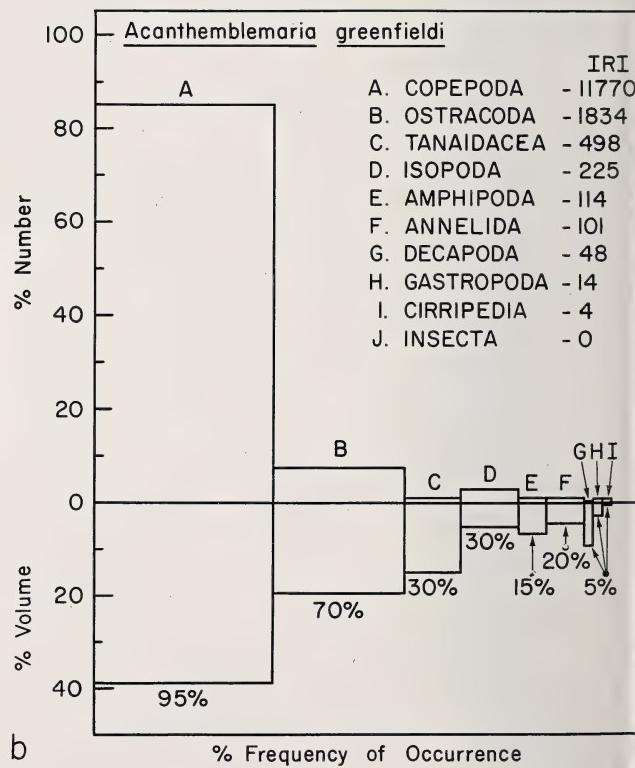
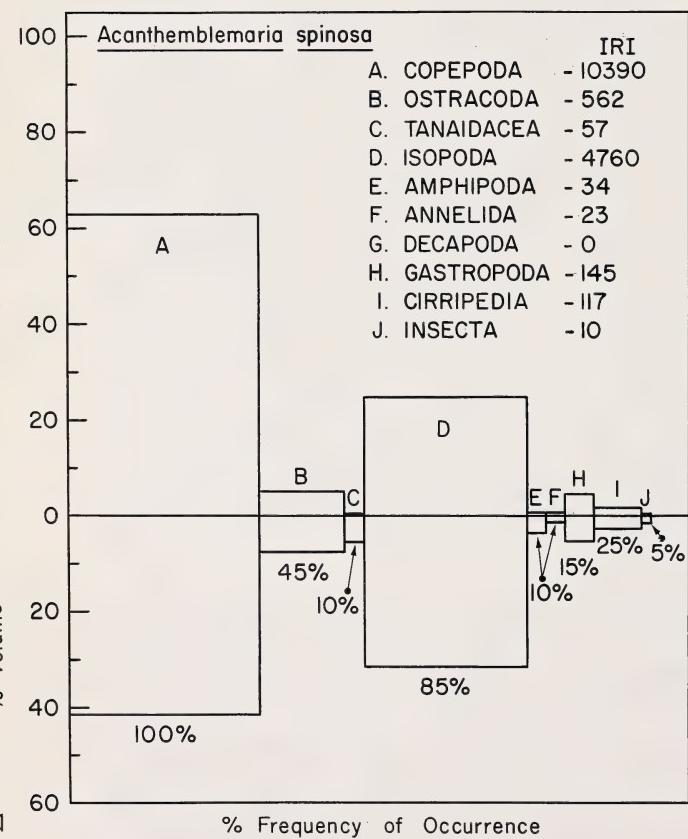


FIGURE 219.—Percent composition of food by taxonomic group in number, volume, and frequency of occurrence in two species of *Acanthemblemaria*: *a*, *A. spinosa*; *b*, *A. greenfieldi*. (IRI = index of relative importance.)

*Emblemaria pricei* Greenfield may occur in the same tree of *Acropora palmata* as *A. spinosa*, but *A. spinosa* is restricted to the basal dead portions and *E. pricei* is found only in holes in the living portion of the coral (Greenfield, 1975:714). *Acanthemblemaria aspera* occurs more commonly on the dead bases of *Montastrea* heads and *Emblemaria pandionis* Evermann and Marsh is found only in a very specific habitat, for instance empty worm or clam holes in small pieces of coral rubble occurring on open sand substrate in areas of moderate current (Greenfield and Johnson, 1981). *Lucayablennius zingaro* (Böhlke), which occurs in deep water, is usually found free-living when feeding (Greenfield, 1972:590).

Examples of fine habitat partitioning among coral-reef fishes in Belize are not restricted to inquiline species. The damselfishes *Eupomacentrus dorsopunicans* (Poey) and *E. diencaeus* Jordan and Rutter both occur at Glover's Reef but are eco-

logically well separated. The first of this pair occurs only in shallow, wave-swept areas on the windward reef, whereas the second occurs only in deeper water or within the lagoon where wave action is absent. *Eupomacentrus diencaeus* also occurs on the reef crest at the leeward side of Glover's Reef, another area where wave action is absent. Nowhere at Glover's Reef have the two species been found occurring in the same area (Greenfield and Woods, 1974:19).

The basslets in the genus *Gramma* provide another striking example of habitat partitioning at the dropoff (fore-reef slope) of the outer fore reef at Glover's Reef. *Gramma loreto* occurs in shallow waters and over the edge of the dropoff to a depth of 24.5 m. A second species, *G. melacara*, occurs from a depth of 21 m on the vertical face of the dropoff down to 110 m. Thus only a 3.5 m zone of overlap occurs at the dropoff at Glover's Reef. Three ichthyocide collections from various depths

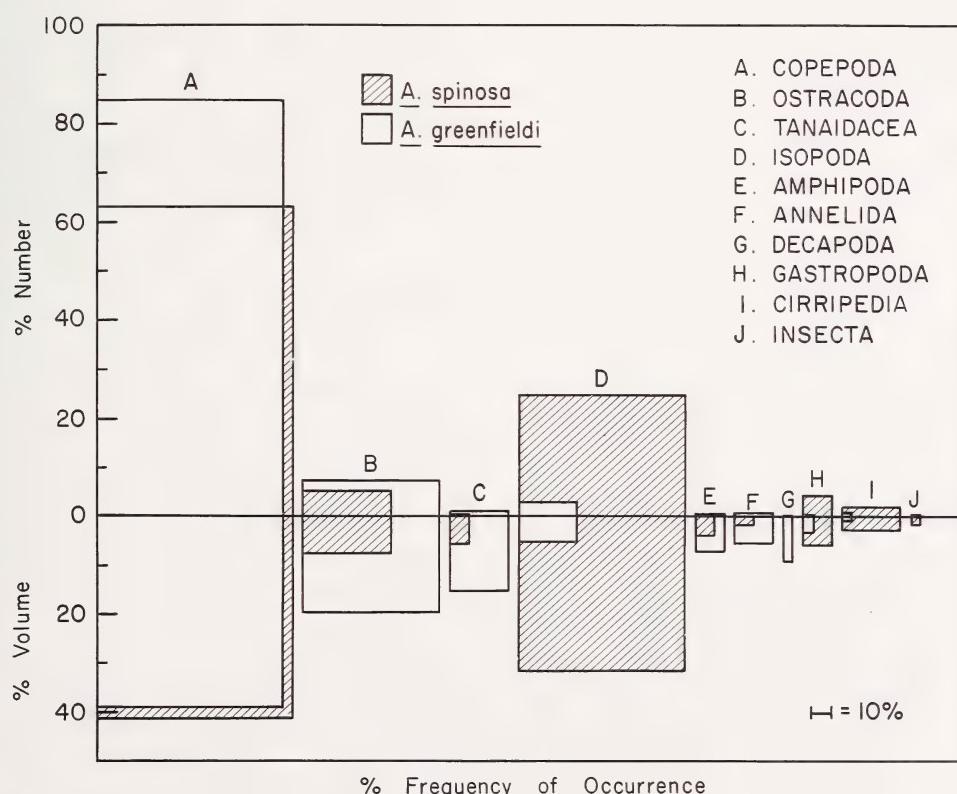


FIGURE 220.—Comparison of percent composition of food by taxonomic group in number, volume, and frequency of occurrence for *Acanthemblemaria spinosa* and *Acanthemblemaria greenfieldi*.

demonstrate the partitioning of habitat by depth: (a) at 18 m, 64 *G. loreto*, 0 *G. melacara*; (b) 21–24 m, 18 *G. loreto*, 91 *G. melacara*; and (c) 34 m, 0 *G. loreto*, 32 *G. melacara*. Colin (1974:37) has observed that the bathymetric distribution of *G. melacara* varies geographically depending upon local conditions, particularly the presence of vertical reef faces. Thus, the sharp separation of *G. melacara* and *G. loreto* is in dropoff areas where strong depth changes occur along relatively short horizontal distances, such as at Glover's Reef. Another species of *Gramma*, *G. linki*, observed at Belize only at the lower depth range of *G. melacara* (Colin, 1974: 34), provides an additional example of habitat partitioning by depth. Starck and Colin (1978: 146) stated that in localities where *G. melacara* is absent, *G. linki* occurs in considerably shallower water.

Since the publication of Sale's work in 1977, several papers have appeared relative to the question of the importance of stochastic larval recruitment of coral-reef fishes. Molles (1978), working in the Gulf of California, found the fish faunas of his small replicate reefs showed a high degree of similarity and a correlation between species diversity and habitat complexity. Gladfelter and Gladfelter (1978) found both a high degree of similarity between fish assemblages and also correlations between assemblages and structural features of a series of relatively large coral patch reefs in the tropical western Atlantic. Gladfelter et al. (1980:1167), recognizing the problems associated with studying colonization in very small artificial structures and the fact that various studies had been conducted by different workers in different oceans, attempted to solve these problems by determining the degree of similarity between fish assemblages of groups of replicate patch reefs in the tropical western Atlantic (Virgin Islands) and in the tropical central Pacific (Marshall Islands). They concluded, "... the high diversity of coral reef fish communities is permitted by a variety of factors other than random recruitment of larvae alone; of these, habitat structure is the most evident."

Anderson et al. (1981:494) presented data on the distribution of butterfly fishes of the northern

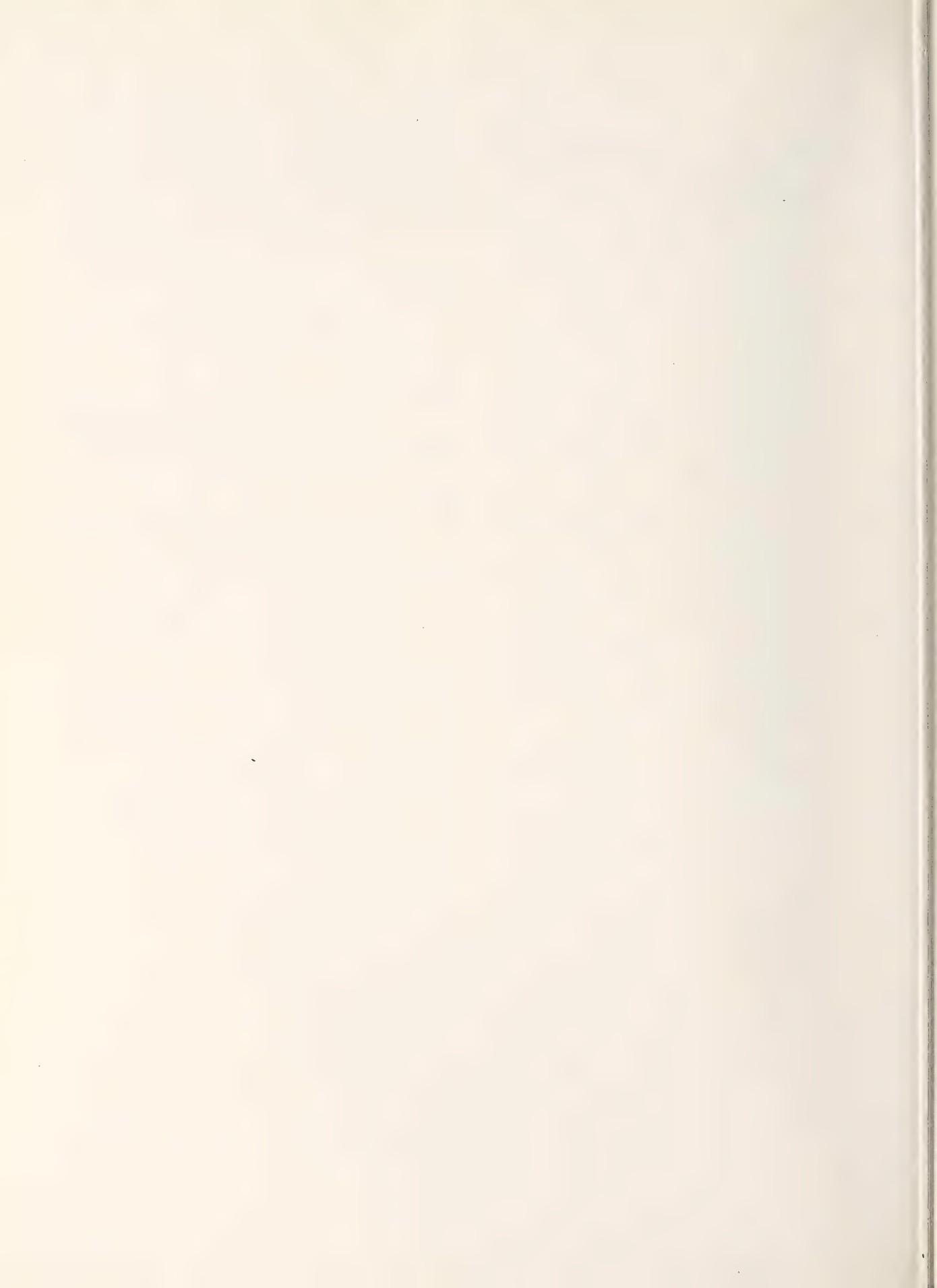
Great Barrier Reefs of Australia in relation to various theories of coral reef fish community structure. They found there were conspicuous niche differences between locally coexisting species, geographical replacement occurred between species from the same niche, and similarities existed between species present at many different sites of the same habitat type. Based on these data they concluded, "Our data do not support the need for alternative hypotheses centered on larval habitat preferences and stochastic recruitment."

Also, additional field work (since the 1977–1978 Carrie Bow Cay observations) has strengthened the findings reported in Greenfield and Johnson (1981) relative to habitat specificity of blennioid fishes.

The examples just cited emphasize the importance of viewing habitat associations of fish species on a sufficiently small scale. The co-occurrence of species from single collections recorded in the literature may often be misleading in suggesting that habitat partitioning is not a reality. Considering that detailed studies have been conducted for only a few species in the western Atlantic Ocean and in the central Pacific, it is premature to conclude that habitat partitioning does not occur among coral-reef fishes. General studies of the blennioid fishes of Belize and Honduras have shown significant differences in species distribution across various major habitat types (Greenfield and Johnson, 1981). Detailed studies of these small species should yield valuable information on the importance of habitat partitioning. Many examples of the absence of habitat partitioning provided by Sale (1977) concerned larger, often herbivorous species; however, the high species diversity found in coral-reef fish communities is largely due to the small sedentary species, such as the blennies and gobies. To date, we have collected over 300 species of reef-associated fishes in Belize, of which 84 are blennies and gobies. Thus, the lottery or chaos hypothesis proposed by Sale may apply to some of the larger species he studied, but it does not appear to apply broadly to all coral-reef fish species in the western Atlantic.

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# Reconnaissance Study of the Geomorphology and Benthic Communities of the Outer Barrier Reef Platform, Belize

Randolph B. Burke

## ABSTRACT

The first general survey of the entire 257 km outer platform of the Belizean barrier reef has disclosed three provinces having distinct community distribution and geomorphic characteristics: (1) the northern province, which contains 46 km of shallow-water reefs; (2) the central province, with 91 km of shallow-water reefs; and (3) the southern province, which includes only 10 km of shallow-water reefs. Central province reefs are the best developed. They are wide and continuous shallow reefs (<-0.2 m MSL) with flourishing communities of branching corals. The fore reef is characterized by high relief and a pronounced ridge, capped with *Acropora cervicornis* at depths of less than 20 m, extending along the shelf edge. The reef in the northern and southern provinces is discontinuous except along Ambergris Cay in the north. Wide passages of uniform depth occur in the northern province, in contrast to the narrow, deep channels within passes typical of the southern province. In both the north and the south, the reef occurs adjacent to islands and generally is more distant from the shelf edge than is the reef along the central province. In the south, however, some sections of the reef occur as reentrants and are closer to the shelf edge.

On the seaward side, framework-building communities have the same composition along the barrier reef, but relative species abundance and density vary significantly. The greatest abundance occurs in the central province in association with the coral ridge and high-relief spur and groove structures. The distribution of these structures coincides with the greatest extent of sea

level reef development. Their distribution also corresponds to the region of the barrier reef most protected from open ocean waves. The shelter afforded by seaward platforms has favored growth of rapidly accumulating communities of branching corals, and thereby has substantially contributed to the central province's development of the most extensive and luxuriant shallow portions of the barrier reef.

## Introduction

Although the longest continuous barrier reef in the West Indies occurs along the continental shelf edge of Belize (Figures 221, 222; Smith, 1971:29) little work has been done on the seaward part of the reef. Previous studies have focused on geological and biological zonations in the lagoon (Wantland and Pusey, 1975). In addition, during the Cambridge Expedition to British Honduras (Thorpe and Stoddart, 1962), Thorpe and Bregazzi (1960) made preliminary observations on corals at Rendezvous Cay. Using their results for baseline data, Stoddart (1962, 1963, 1969, 1974) studied hurricane damage to the reef and subsequent recovery. York (1971) compiled a photolog of common Belizean corals. Recent geologic studies on the deep seaward margin (James and Ginsburg, 1978) and studies of shallow-water submarine cementation (James et al., 1976) have described parts of the windward section of the barrier reef.

This paper presents a comprehensive survey of the Belizean barrier reef based largely on aerial reconnaissance and underwater observations. It

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FIGURE 221.—Belizean barrier reef looking south towards Tobacco Cay entrance, an example of the extensive shallow-water reef development characteristic of the central province.

thus places the Carrie Bow Cay transect data (see Rützler and Macintyre, herein: 9) into regional perspective. The study considers shelf bathymetry, regional patterns of wave energy, and the distribution and development of reef communities and their architecture.

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Union Oil Company. I. Jewett drafted the final version of the figures.

### Methods

Low altitude aerial photography was used to map major geomorphic features and reef communities along the margin of the Belizean barrier reef platform from Ambergris Cay in the north to Zapotilla Cays in the south. Surveys by SCUBA diving were also made along seven transects perpendicular to the reef to record the bottom profile and zonation of substrates and organisms (Figure 222).

Photographs were taken through the open window of a high-wing plane at an altitude of 150 m and air speed of 160–170 km/h, using 35 mm and 60 mm cameras equipped with polarizing filters. Pictures were taken between 0900 h and 1500 h when glare was at a minimum. Two photographic

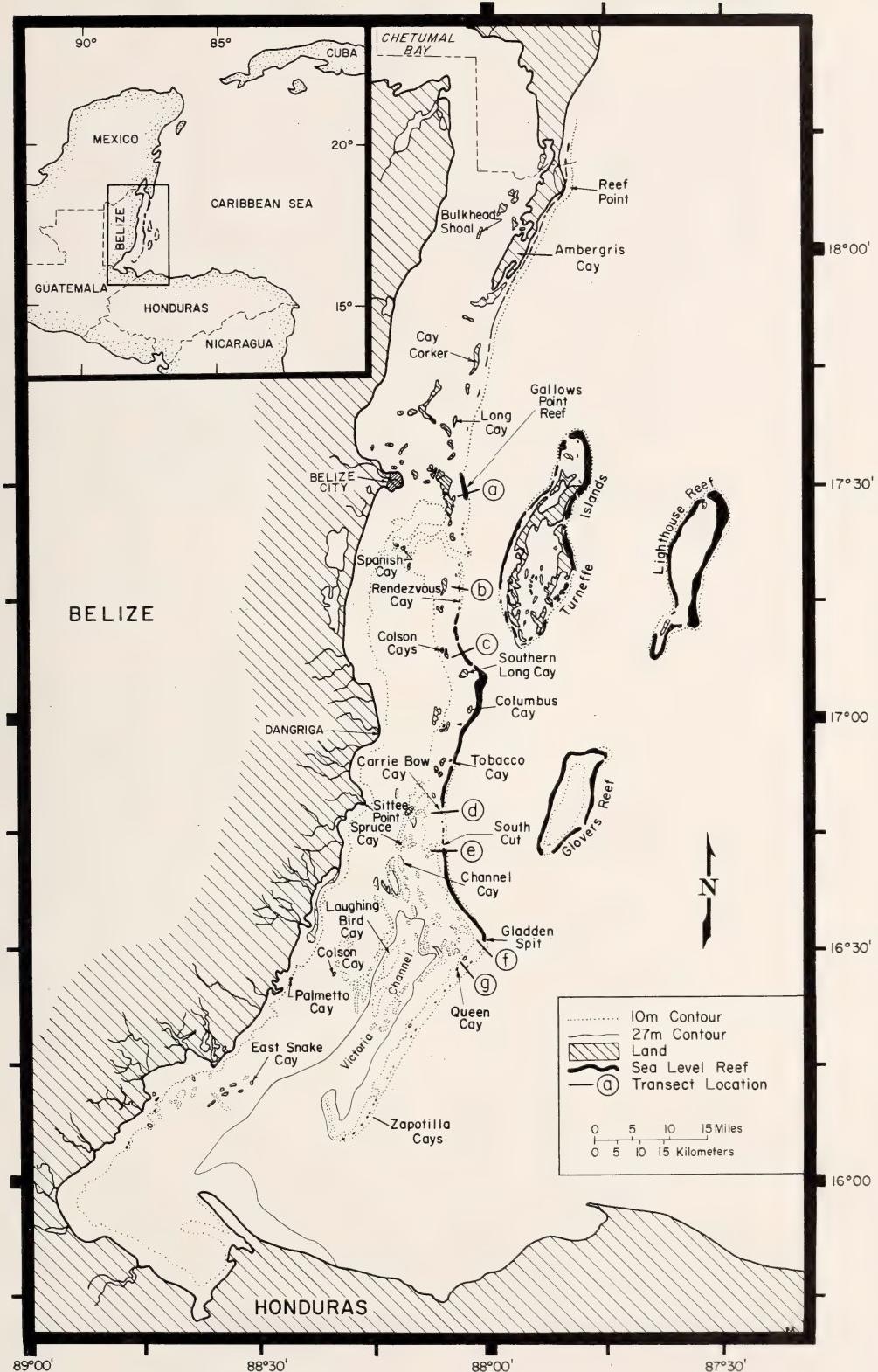


FIGURE 222.—Map of the coastal areas of Belize showing distribution of sea level reefs, as determined by this study, and location of transects (a-g).

surveys were flown, the initial one concerned primarily with establishing transect sites. After ground truth transects were completed, the second photography flight documented their location. Calm water after a norther improved visibility through the water, and thus provided reliable resolution to depths of 20 m for mapping the geomorphic features and the principal bottom communities.

The underwater transects, measured with depth gauges and from charts, extended from the lagoon, across the reef crest, and down the shelf edge to depths of 40 m. Dominant biota and visual estimates of percentage of cover were recorded on mylar sheets attached to a PVC wrist slate. In addition, characteristic zones of the transects were photographed. Wave energy was calculated from mean annual wind direction and wave heights resolved from SSMO (Snyoptic Summary of Meteorological Observations) data (United States Naval Weather Service Command, 1974). See Burke (1979) for details on wave energy calculations.

### Composition and Distribution of Major Reef Structures

#### PHYSIOGRAPHIC PROVINCES

The barrier reef platform (<5.5 m depth) seaward of Belize is 257 km long, of which 147 km consists of shallow-water reefs (<0.2 m depth; Figure 222). The remainder of the shelf-edge platform is cut by channels or is composed of carbonate shoals, fleshy-algae-covered pavements, or deeper reef development. The reef complex can be divided into three provinces on the basis of community distribution and geomorphic characteristics: the northern, central, and southern provinces. The biological and topographic characteristics of these provinces are defined as follows.

**NORTHERN PROVINCE.**—Extending approximately 78 km southward from Reef Point to the northern tip of Gallows Point Reef, this province includes approximately 46 km of reef and the muddy, shallow Chetumal Bay-lagoon complex

with average water depth less than 6 m. The barrier platform in this province is distinguished by a line of mangrove cays set well inside the shelf edge. Passes between the reef and these islands are wide and shallow ( $\leq 5$  m deep). Except for areas along Ambergris Cay and Cay Corker where the reef crest is formed by *Millepora*-coralline mounds or coralline-algae-encrusted corals, the area of the reef crest and inner fore reef in the northern province has few living corals and is rounded and gently sloping. Coral is abundant behind the reef crest along Ambergris Cay (Plate 1: *top left*). The shoals between this cay and Gallows Point are primarily a pavement covered by rubble, sand, and only sparse corals. The biota along the shelf-edge break are luxuriant except where numerous wide sand channels cross the shelf and are probably similar in composition to biota along the shelf break at Gallows Point Reef (see Figure 223a).

**CENTRAL PROVINCE.**—Extending south approximately 120 km from Gallows Point Reef to Gladdden Spit, this province has more than 91 km of shallow-water reef (Figure 221; Plate 1: *top right, center left*); and includes the central and southern lagoons, which have depths of less than 27 m. Numerous mangrove cays occur near the center and landward side of the barrier platform, and along the boundary of the southern lagoon. Unique to the central province are a few sand cays built on the inner edge of the shallow-water reef, and three carbonate platforms 8 to 40 km seaward: Turneffe Islands, Lighthouse Reef, and Glover's Reef (Figure 222). In contrast to the others, the central province of the barrier platform supports long and wide sections of uninterrupted reef, which are cut by only two major channels and scattered narrow passes. The central province is characterized by three distinct structural features: high-relief spur and groove zones, double high spur and groove zones, and a shelf-edge coral ridge (Figure 224).

The high-relief spur and groove system occurs over 52 km of the reef. The relief of spurs ranges from 2 m to more than 10 m; spurs are dominated by coral communities in less turbulent water and by *Millepora*-coralline algae in higher wave en-

ergy zones. A double high-relief spur and groove system occurs over 16 km of the reef and is separated from the reef crest by a channel that runs parallel to the reef trend and contains boulder rubble. The communities on these spurs are rich in coralline algae and *Millepora complanata* Lamarck.

Coral ridges occur along 48 km of the outer reef at the shelf edge and are capped by *Acropora cervicornis* (Lamarck) at depths less than 20 m. At depths greater than 20 m, the ridge is less continuous and less wide; *A. cervicornis* becomes less abundant and platy corals, particularly *Montastrea annularis* (Ellis and Solander), prevail. Ridges having high relief occur only leeward of the seaward platforms.

**SOUTHERN PROVINCE.**—Extending approximately 59 km from Gladden Spit to Zapotilla Cays, this province has about 10 km of shallow-water reef and a deep lagoon (>27 m deep), which is known as Victoria Channel. The barrier platform supports a few small cays in this province, most of which are well inside the shelf edge. Passes are wide and generally have narrow, deep channels (6–10 m deep). In passes, the platform crest is broad and rounded and supports a dense crop of algal macrophytes.

In the southern province, shallow-water reefs occur only as fringe around islands and reentrants to the lagoon. The reef crest is composed mainly of weakly coalesced *Millepora*-coralline mounds and rubble. Coral density is greatest in the back reef and along the shelf edge.

#### TRANSECTS ACROSS THE BARRIER REEF

Seven underwater transects are described from north to south: five in the central province, and two in the southern (Figures 222, 223). Descriptions proceed from the lagoon to the shelf edge. Gallows Point Reef is described in detail as a reference for the remainder of the transects. Constituents change little between transects, but population densities and areal distributions vary markedly.

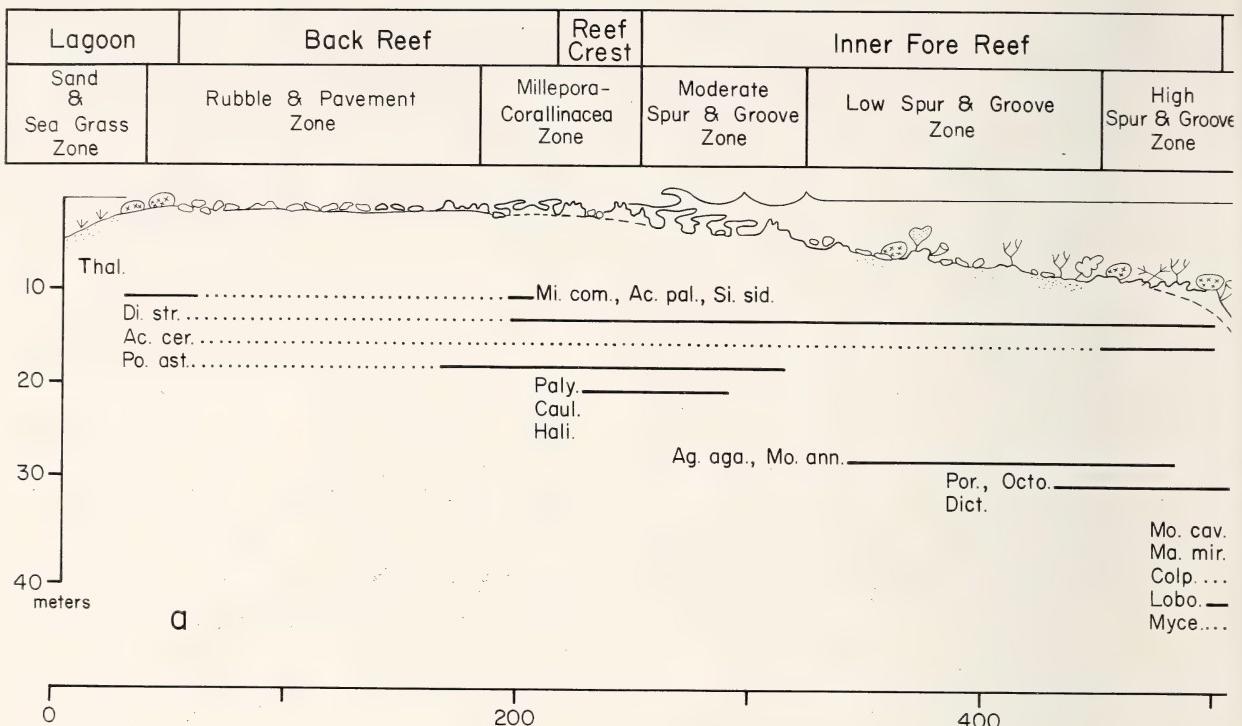
**GALLONS POINT REEF, CENTRAL PROVINCE** (Figure 223a).—Almost due east of Belize City, Gal-

lows Point Reef is the northernmost transect. A *Thalassia*-dominated lagoon grades into reef-derived rubble that surrounds patch reefs which fringe the moderately gentle back-reef slope. Common constituents of the patch reefs are the corals *Siderastrea radians* (Pallas), *S. siderea* (Ellis and Solander), *Porites astreoides* (Lamarck), *Favia fragum* (Esper), *Agaricia* sp., *Diploria clivosa* (Ellis and Solander), *D. strigosa* (Dana), and the hydrozoans *Millepora alcicornis* Linnaeus and *M. complanata*. The rubble is interrupted locally by pavement covered with algal turf and by sand patches. *Hydrolithon boergesenii* (Foslie) Foslie, and a few species of *Neogoniolithon* are common encrusting corallines on back-reef rubble. On the turf-covered pavement, dominated by microscopic algae (<1 cm)—primarily *Phaeophyta* and *Rhodophyta* that stabilize a sediment veneer—there is an increasing abundance of *Porites astreoides* and coralline algal mounds toward the reef crest.

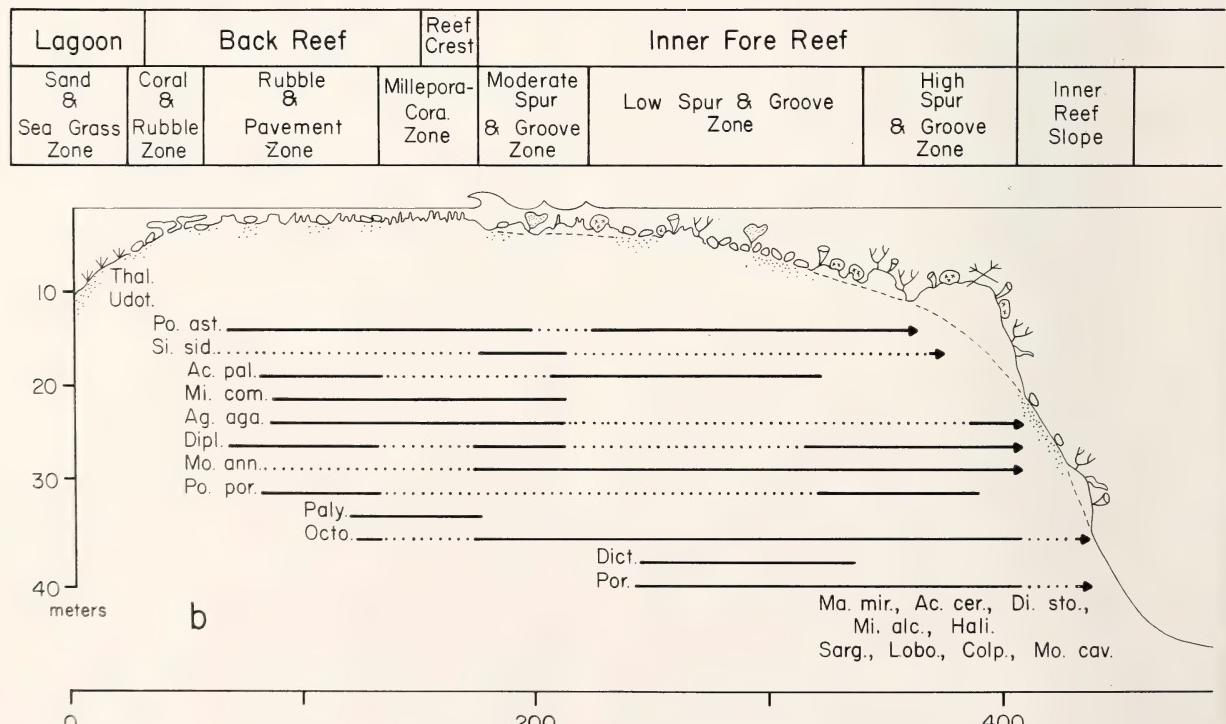
The somewhat elongate, steep-sided (0.5 m high) mounds of the reef crest, dominated by *Millepora complanata* and crustose corallines, support diverse biota, including the zoanthid *Palythoa* sp., *Porites astreoides*, *Favia fragum*, *Siderastrea siderea*, *Caulerpa* sp., *Halimeda* sp., and a few *Diploria clivosa*, *D. strigosa*, *Agaricia* sp., and *Acropora palmata* (Lamarck). A patchwork of pavement with some rubble, coated by both corallines and algal turfs, surrounds the mounds. Coralline algae encrusting the rubble include *Porolithon pachydermum* (Weber-van Bosse and Foslie in Foslie) Foslie and *Neogoniolithon* sp.

Scattered thickets of *Acropora palmata* commonly interfinger with the reef crest and the spur and groove zone of the fore reef. Rubble is a major component in the sand-floored grooves and on the turf-covered pavement. Like the reef crest, the surface of the spurs supports a variety of corals, predominantly *A. palmata*, *Montastrea annularis*, *Agaricia agaricites* (Linnaeus), and *Porites astreoides*. Seaward, on the low-relief spur and groove pavement, rubble is commonly covered by the encrusting sponge *Cliona* sp. and other encrusting organisms such as the coralline algae *Paragoniolithon* sp., *Neogoniolithon* sp., and some *Tenarea prototype* (Foslie) Adey. Along with the pavement, the rub-

## Gallows Point Reef



## Rendezvous Cay



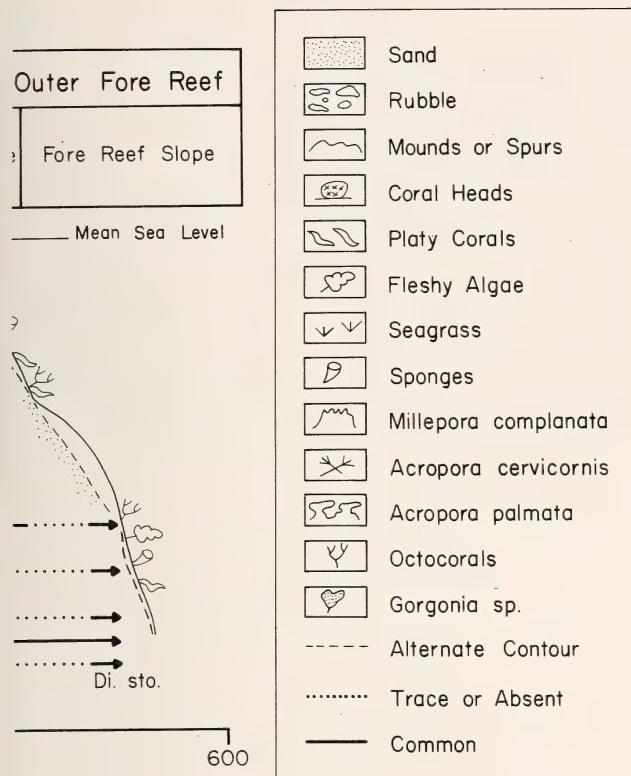
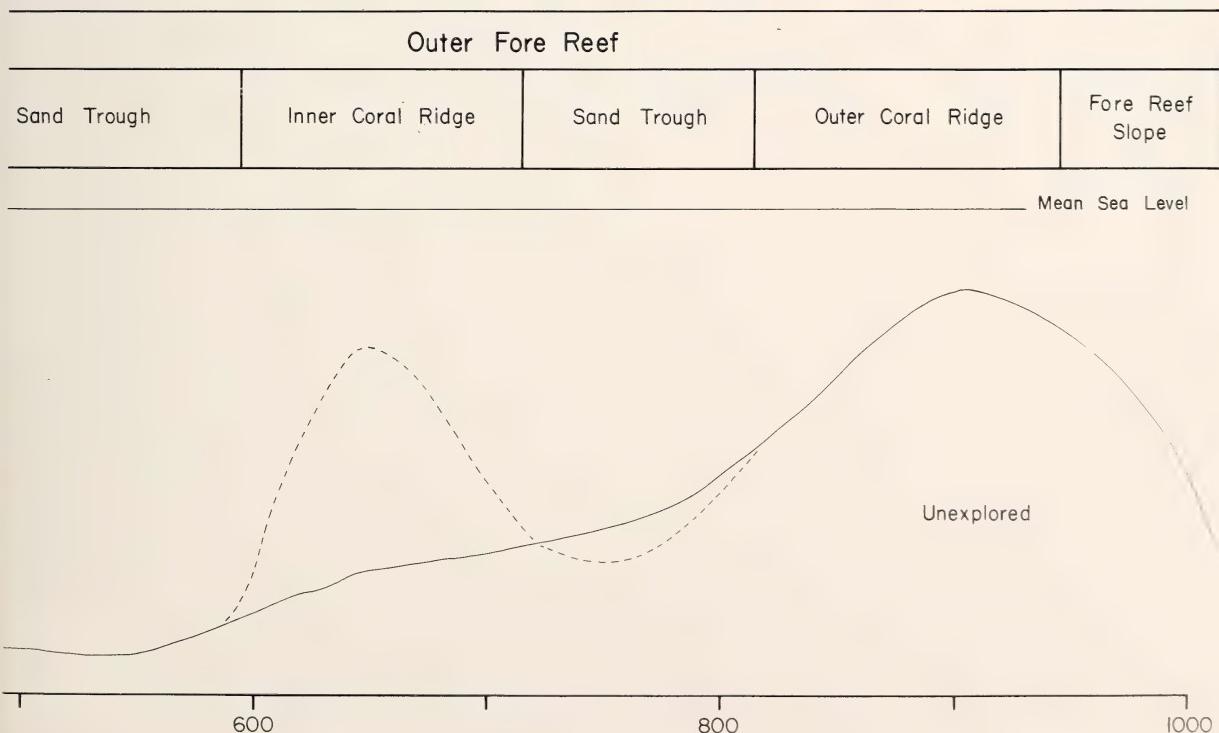
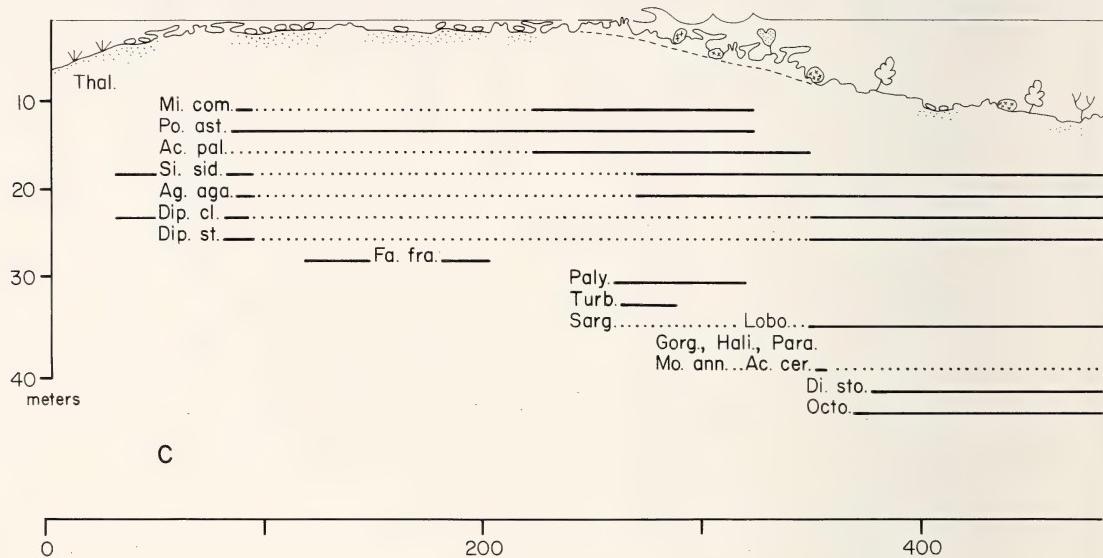


FIGURE 223.—Idealized sketches of barrier reef transects (located in Figure 222), showing reef zonation and major components of surface coverage: *a*, Gallows Point Reef; *b*, Rendezvous Cay (configuration of coral ridges determined from hydrographic charts and aerial reconnaissance); *c*, Colson Cay (the inner coral ridge is a branch of the outer ridge, not a parallel structure); *d*, Carrie Bow Cay (after Rützler and Macintyre, herein, Table 1, Figures 4, 5); *e*, South Cut; *f*, Gladden Spit (shelf edge not observed, dashed profile taken from hydrographic charts); *g*, Queen Cay. (Coverage indicated by location of abbreviation and solid or dotted lines; arrowheads mark extended distribution; abbreviations: Ac. cer. = *Acropora cervicornis*, Ac. pal. = *A. palmata*, Ag. aga. = *Agaricia agaricites*, Caul. = *Caulerpa* sp., Colp. = *Colpophyllia* sp., Cora. = *Corallinacea*, Di. sto. = *Dichocoenia stokesi*, Dict. = *Dictyota* sp., Dip. cl. = *Diploria clivosa*, Dip. la. = *D. labyrinthiformis*, Dip. st. = *D. strigosa*, Dipl. = *Diploria* sp., Fa. fra. = *Favia fragum*, Gorg. = *Gorgonia* sp., Hali. = *Halimeda* sp., Lobo. = *Lobophora* sp., Ma. mir. = *Madracis mirabilis*, Me. mea. = *Meandrina meandrites*, Mi. alc. = *Millepora alcicornis*, Mi. com. = *M. complanata*, Mille. = *M. sp.*, Mo. ann. = *Montastrea annularis*, Mo. cav. = *M. cavernosa*, Myce. = *Myctophyllia* sp., Octo. = *Octocorallia*, Padi. = *Padina* sp., Paly. = *Palythoa* sp., Para. = *Paragoniolithon* sp., Por. = *Porifera*, Po. ast. = *Porites astreoides*, Po. por. = *P. porites*, Sarg. = *Sargassum* sp., Scol. = *Scolymia* sp., Si. rad. = *Siderastrea radians*, Si. sid. = *S. siderea*, Sid. = *Siderastrea* sp., Styp. = *Styptodium* sp., Turb. = *Turbinaria* sp., Thal. = *Thalassia* sp., Udot. = *Udotea* sp.)



## Colson Cay

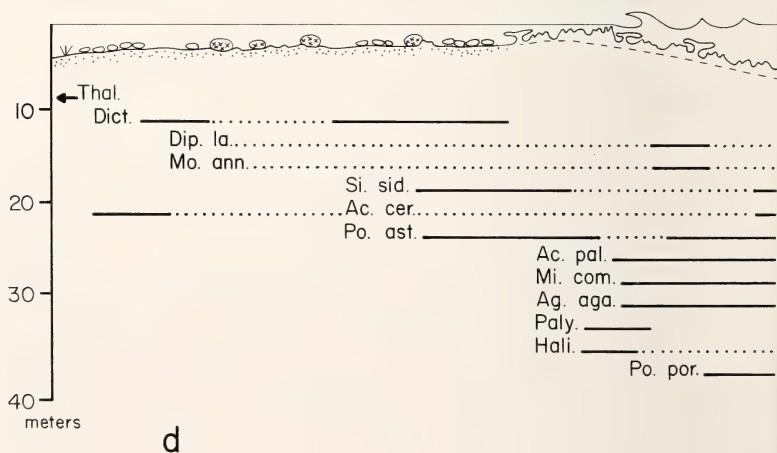
Lagoon		Back Reef		Reef Crest	Inner Fore Reef	
Sand & Sea Grass Zone	Rubble & Coral Zone	Rubble & Pavement Zone		Millepora-Cora. Zone	Moderate Spur & Groove Zone	Low Spur & Groove



C

## Carrie Bow Cay

Lagoon		Back Reef		Reef Crest	
Sand & Sea Grass Zone	Sand & Rubble Zone	Patch Reef Zone	Rubble & Pavement Zone	Millepora-Cora. Zone	High Spur &

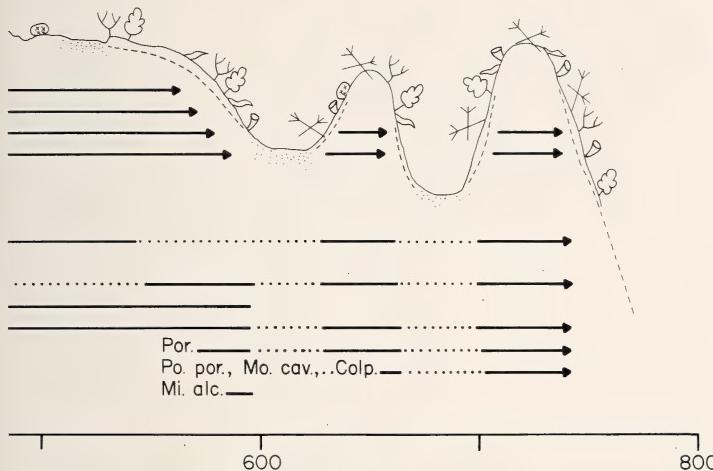


d



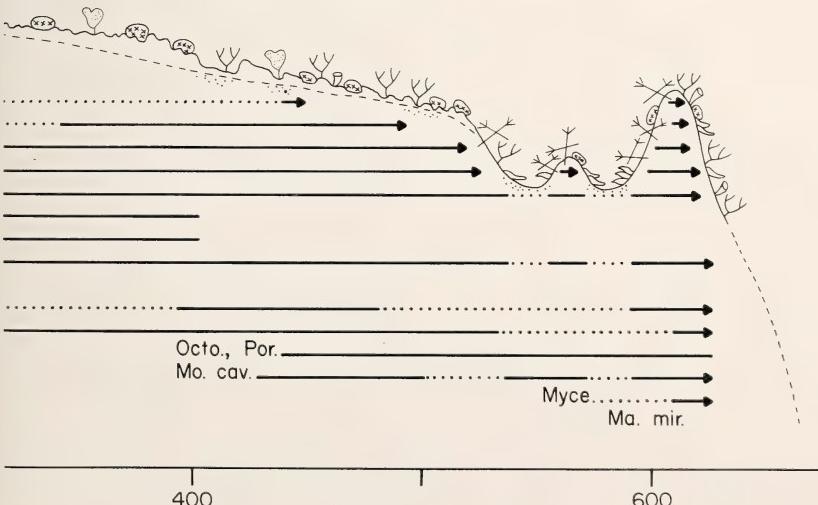
	Outer Fore Reef			
Zone	Inner Reef Slope	Sand Trough & Inner Coral Ridge	Outer Coral Ridge	Fore Reef Slope

Mean Sea Level



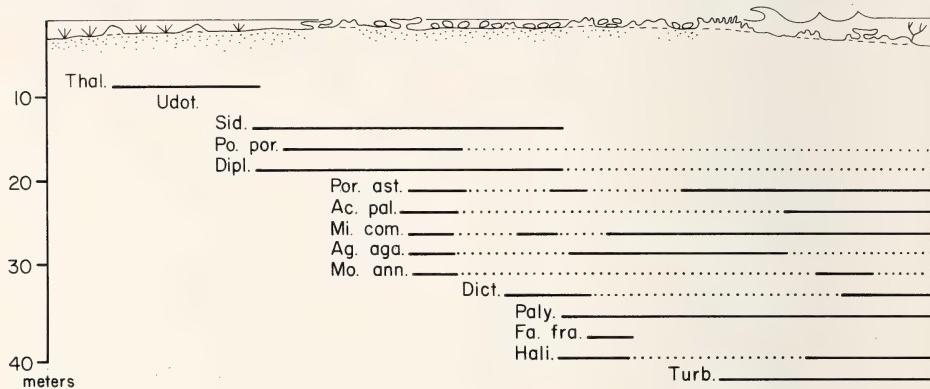
Inner Fore Reef		Outer Fore Reef			
Groove Zone	Low Spur & Groove Zone	Inner Reef Slope	Sand Trough	Outer Coral Ridge	Fore Reef Slope

Mean Sea Level



## South Cut

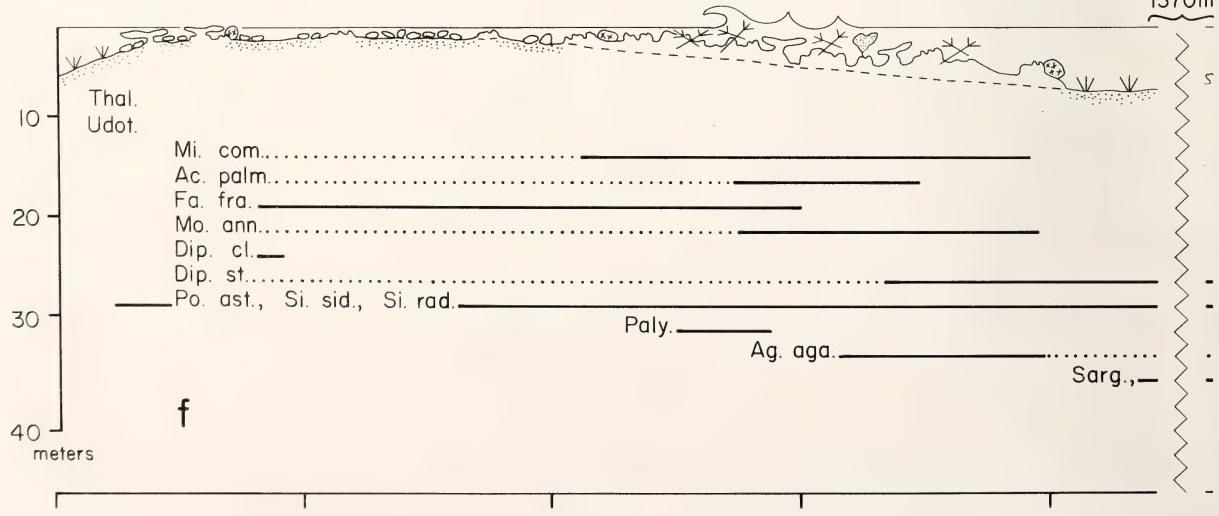
Lagoon	Back Reef		Reef Crest	
Sand & Sea Grass Zone	Rubble & Coral Zone	Rubble & Pavement Zone	Millepora-Corallinacea Zone	Spur & Groove Zone



e

## Gladden Spit

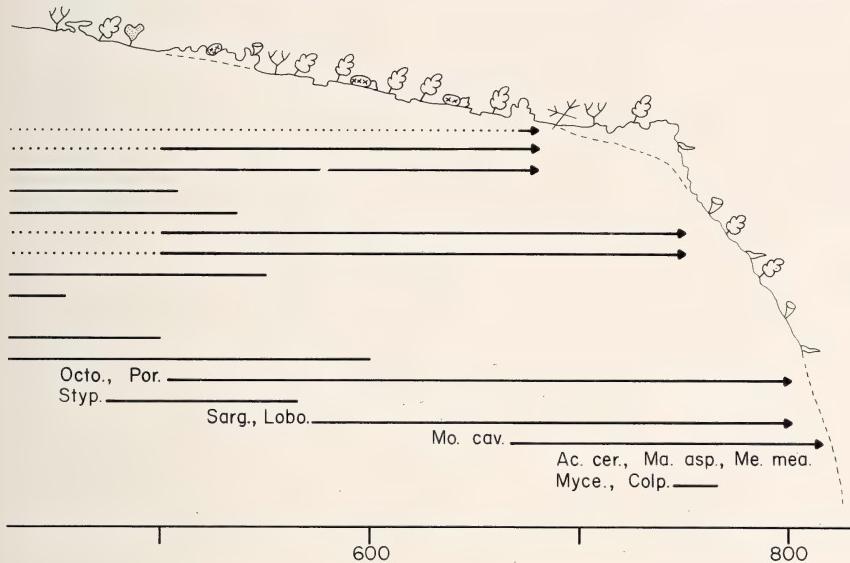
Lagoon	Back Reef		Reef Crest	
Sand & Sea Grass Zone	Rubble & Coral Zone	Millepora-Corallinacea Zone	Moderate Spur & Groove Zone	



f

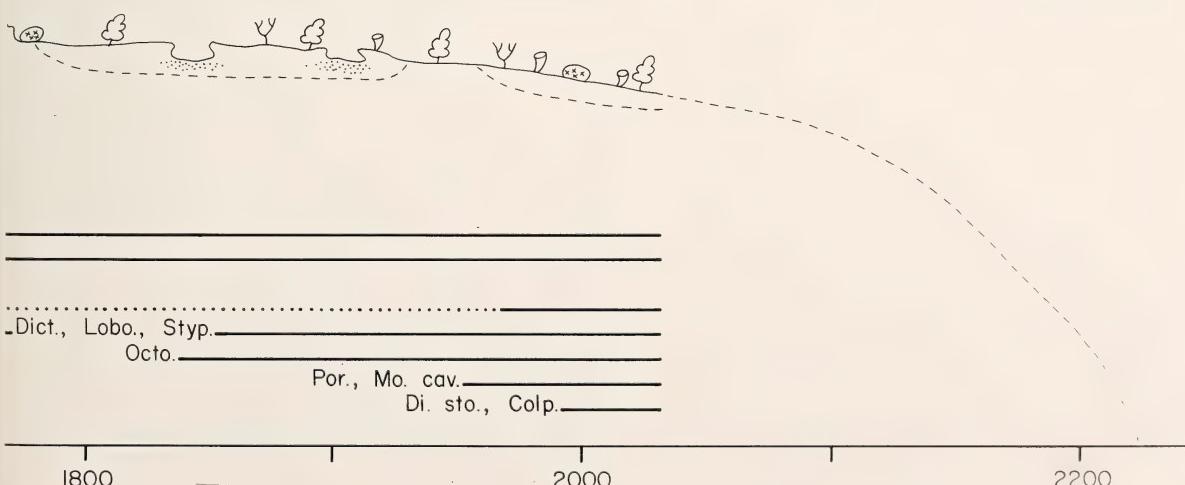
Inner Fore Reef			Outer Fore Reef	
Pavement Zone	Mod. Spur & Groove Zone	Pavement Zone	High Spur & Groove Zone	Fore Reef Slope

Mean Sea Level



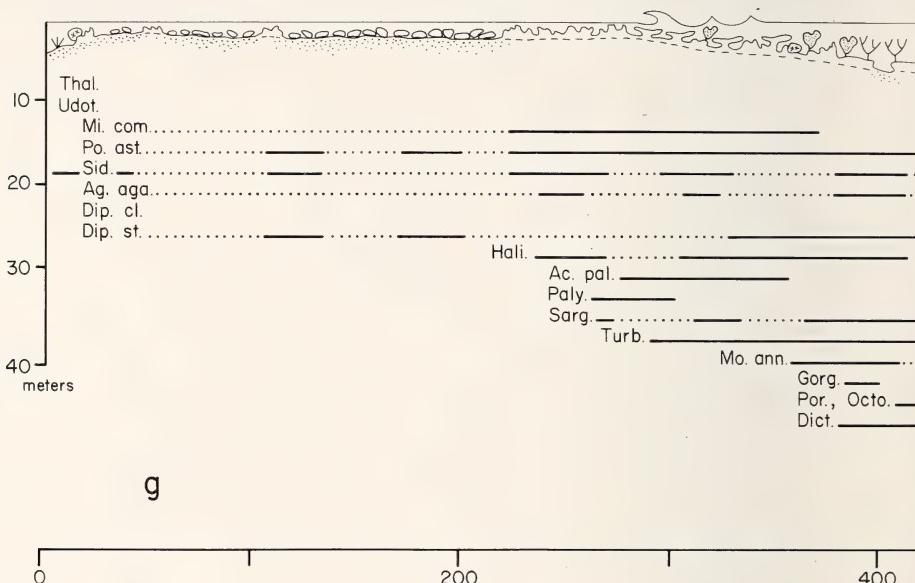
Inner Fore Reef	Outer Fore Reef
Pavement & Sand Channel Zone	Fore Reef Slope

- Mean Seq Level



## QUEEN CAY

Lagoon		Back Reef	Reef Crest
Sand & Sea Grass Zone	Rubble & Coral Zone	Rubble & Pavement Zone	Mille-Cora. Zone



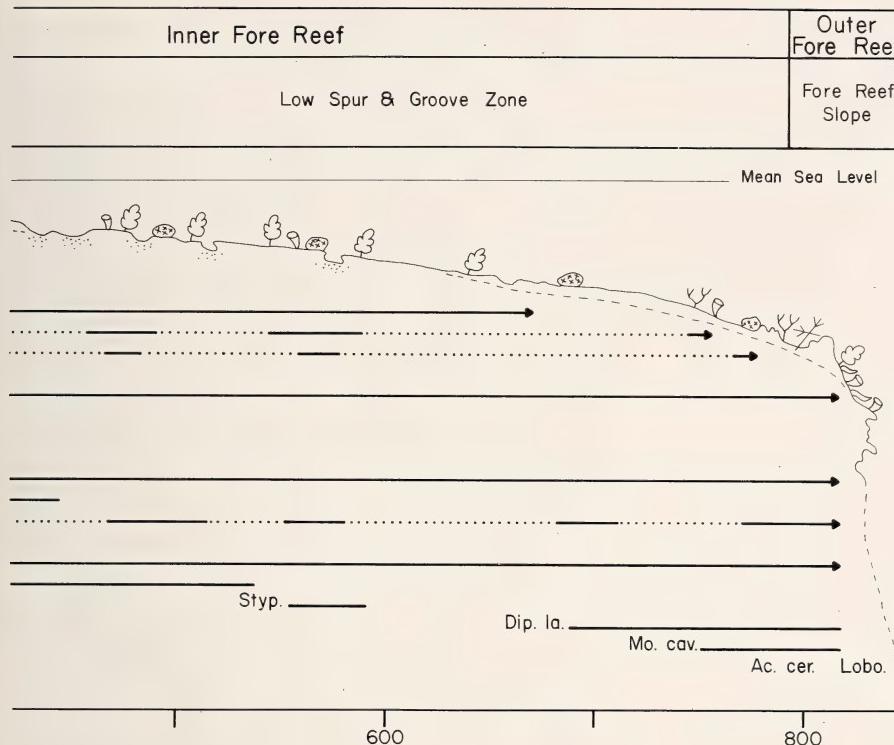
ble provides the primary substrate for the ubiquitous alga *Dictyota* sp., the common *Gorgonia* sp., other octocorals, sponges, and diverse but scattered coral heads, mostly *Diploria strigosa* and *Montastrea annularis*.

Near the shelf edge, a weakly developed spur and groove system with about 1.5 m relief marks the transition to the fore-reef slope. Spurs along the seaward face are characterized by a rather dense (approaching 50 percent cover) and diverse coral assemblage in which *Montastrea cavernosa* (Linnaeus), *M. annularis*, and *Agaricia* spp. are most abundant. Corals common to deeper water, such as *Mussa angulosa* (Pallas), *Mycetophyllia* sp., *Madracis mirabilis* (Duchassaing and Michelotti), and *Colpophyllia* sp. are also conspicuous, together with sparse populations of *Acropora cervicornis*, *Diploria labyrinthiformis* (Linnaeus), *D. strigosa*, and *Siderastrea siderea*. Turf and the alga *Lobophora* sp. are most abundant, but large vase sponges and octocorals are also common.

At the base of the spur faces a pavement slope is coated with a thin veneer of fine sand and

abundant *Lobophora* sp., but as the slope steepens, corals again dominate and in places form local overhangs along the shelf-edge wall.

RENDEZVOUS CAY, CENTRAL PROVINCE (Figure 223b).—This transect lies 2.2 km north of Rendezvous Cay on the outer barrier reef. The shallow reef is narrow here and the back-reef slope is steep, rising abruptly 10 m from a sand bottom having seagrass and algae (*Udotea* sp., *Penicillus* sp., and *Padina* sp.). A distinct rubble zone lies immediately below the patchy but dense colonies of *Acropora palmata* and mounds of *Millepora complanata*, *Montastrea annularis*, and *Siderastrea siderea* that span the sharp slope of the back reef. Turf-covered rubble dominates the back-reef flat, which also has a sparse coral fauna that includes *Porites astreoides*, *Agaricia agaricites*, *Diploria* sp., and *P. porites* (Pallas). *Palythoa* sp. coats the rubble crest where *Millepora*-coralline mounds constitute less than 40 percent of the crest's irregular trend. Rubble continues to predominate through the moderately high-relief (1.3 m) spur zone in which *Montastrea annularis* is the principal coral. Less



abundant species include *Isophyllastrea rigida* (Dana), *Dendrogyra cylindrus* Ehrenberg, and *Acropora palmata*. Turf, *Dictyota* sp., and fine sediment cover much of the low-relief spur and groove pavement as the amount of rubble decreases seaward. The rubble consists primarily of branches of *Acropora cervicornis*. *Pseudopterogorgia* sp., *Gorgonia* sp., other octocorals and sponges are the most conspicuous components of the pavement, which also includes the corals *Dichocoenia stokesi* (Milne Edwards and Haime) and *Dendrogyra cylindrus*.

Massive spurs of up to 4.8 m relief mark the slope break, which drops to 44 m into a sand trough. Upper spurs are characterized by scattered *Acropora cervicornis*, *Madracis* sp., *Porites porites*, *Montastrea annularis*, and *M. cavernosa* and abound with octocorals and sponges. Coral diversity is highest on the seaward face, which also supports *P. astreoides*, *Mycetophyllia* spp., *Colpophyllia* sp., *Isophyllia* sp., *Diploria labyrinthiformis*, *Eusmilia fastigiata* (Pallas), and encrusting *Millepora alcicornis* on octocorals. *Lobophora* sp. is more common on horizontal surfaces and *Halimeda* spp. on spur

margins. Depths between 20 and 35 m are characterized by a sandy slope having patches of raised pavement that support the alga *Sargassum* sp., octocorals, and large vase sponges.

Aerial reconnaissance revealed two large ridge systems bordering the shelf edge which were not seen during the dive because of turbid water. The ridges could be comparable to the *Acropora cervicornis*-capped coral ridges at Colson and Carrie Bow cays (see below). These ridges, however, are more segmented and, according to hydrographic charts, have up to 35 m of relief.

**COLSON CAY, CENTRAL PROVINCE** (Figure 223c).—Lagoon and back-reef areas are similar to Gallows Point although sand patches are more common within the rubble of the back reef. A discontinuous series of *Millepora*-coralline mounds mark the reef crest, which is composed of over 60 percent rubble. Rubble coverage increases to over 70 percent in an irregular zone that enters the spur and groove system. Algal biomass on the crest approaches 450 g/m<sup>2</sup> and is composed mainly of *Sargassum* sp. and *Turbinaria turbinata*

(Linnaeus) Kuntze. *Lobophora* sp. and *Halimeda* sp. become the primary algal macrophytes on the turf-dominated rubble zone that separates the reef crest from the adjacent spur and groove zone.

Living corals in this spur and groove zone cover less than 10 percent of the surface. Rubble, prevalent in grooves, is covered mainly by turf, the coralline alga *Paragoniolithon* sp., and *Lobophora* sp. The most obvious coral is *Acropora cervicornis* with some *Montastrea annularis*, *Agaricia agaricites*, *Siderastrea siderea*, and only a few patches of *Acropora palmata*. These spurs of moderate relief grade seaward into a low-relief spur and groove system covered primarily by fine sediment stabilized by turf and a scattering of *Sargassum* sp. The few corals present are scattered widely. Coral diversity and numbers increase on steeper spur faces at the slope break. At the base of the spur face, the bottom is about 50 percent low-relief spurs and the remainder is sand. Whip-like octocorals are abundant, as are several types of large sponges.

An anastomosing coral ridge, capped by *Acropora cervicornis* and separated from the inner fore reef by a sand trough, characterizes the outer fore reef and shelf edge. This ridge, which does not appear on hydrographic charts, has a maximum relief of 16 m. *Lobophora* sp. is common in the areas of pavement, which, along with dead branches of *A. cervicornis*, serve as attachment sites for the abundant octocorals, a variety of vase sponges, and less conspicuous corals such as *Madracis asperula* Milne Edwards and Haime, *Colpophyllia* sp., *Montastrea cavernosa*, *Mycetophyllia* sp., *Isophyllia sinuosa* (Ellis and Solander), and *Scolymia* sp.

CARRIE BOW CAY, CENTRAL PROVINCE (Figure 223d).—This is the IMSWE Program reference transect, which is described in detail in Rützler and Macintyre (herein: 9).

SOUTH CUT, CENTRAL PROVINCE (Figure 223e).—The transect traverses the barrier reef on the south side of the South Cut reentrant (Figure 222). Rubble dominates the immediate back reef, which grades into a crest of sparse mounds of *Millepora* and coralline algae. The crest is composed of about 50 percent rubble. Fine sediment

stabilized by turf covers most hard surfaces, with *Neogoniolithon* sp., some *Porolithon pachydermum*, and *Millepora complanata* present on higher areas. Fleshy algal macrophyte coverage is relatively low ( $<100 \text{ g/m}^2$ ) and consists mainly of *Turbinaria* sp. *Palythoa* sp. forms mats over less than 3 percent of the area. A series of low-relief ( $<1 \text{ m}$ ) spurs surrounded by rubble extends below the crest. Biota on the spurs are similar to that found on the crest, but some *Agaricia agaricites*, *Acropora palmata*, and *Halimeda* spp. also occur.

The number and size of the spurs and mounds decrease seaward of the crest. The mounds broaden into a pavement covered primarily by turf, rubble, and sand. *Gorgonia* sp., other octocorals, and the alga *Stylopodium* sp. are the most conspicuous components, but are quantitatively unimportant in terms of surface coverage. Another set of mounds occurs at a depth of about 6 m and in places they coalesce to form a moderately high-relief ( $\approx 4.5 \text{ m}$ ) spur and groove system. *Acropora palmata*, *Agaricia agaricites*, *Millepora complanata*, and an encrusting *Millepora* sp. are the most obvious components, although turf with sediment, *Sargassum* sp., and *Lobophora* sp. are actually more abundant ( $\approx 200 \text{ g/m}^2$ ).

Near the slope break, coral and octocoral densities increase as mounds of *Montastrea annularis* ( $\approx 1 \text{ m}$  high) mark the transition into the high-relief ( $\approx 4.5 \text{ m}$ ) spur and groove zone. Common corals are shown in Figure 223e. *Porites astreoides*, *P. porites*, and *Acropora cervicornis* are most abundant along groove margins. *Madracis asperula* occurs principally along the spur faces.

Turf-covered pavements with abundant *Lobophora* sp. broaden from the base of the spurs. These hardgrounds constitute almost 30 percent of the fore-reef slope, the remainder being steep sandy slopes that include some coral rubble. The hard bottom supports numerous large vase sponges and scattered coral, mainly of the species *Montastrea cavernosa*, *Colpophyllia* sp., *Meandrina meandrites* (Linnaeus), *Mycetophyllia* sp., *Agaricia* sp., and *Scolymia* sp.

GLADDEN SPIT, SOUTHERN PROVINCE (Figure 223f).—The barrier reef bends around Gladden

Spit and consists of large patch reefs that rise from a turf and fleshy-algae-covered pavement with sand channels. From here southward, the shallow-water reef is absent except as island fringes and reentrants. The transect crosses a large patch reef on the south side of Gladden Spit that has a segmented, locally emergent reef crest approximately 400 m long.

Lagoon and back-reef areas are similar to those at Rendezvous Cay. Rubble constitutes 40 to 60 percent of the reef surface across the crest and continues through the moderate-relief spur and groove zone. The rubble is composed mainly of branches of *Acropora palmata* ( $\approx$ 0.5 m long). Turf is the main cover along with the encrusting alga *Neogoniolithon* sp.; however, *Porolithon pachydermum* is also common. *Millepora complanata* and *Palythoa* sp. dominate the mounds on the reef crest. As the mounds grade into spurs, *Acropora palmata* and *Agaricia agaricites* become the most obvious components on spur margins. Knobby pillars of *Montastrea annularis* ( $\approx$ 2 m high) increase in abundance where the spurs begin to break up and decrease in size as they grade into a pavement with sand channels.

Fleshy algal macrophytes are dominant on the pavement and increase in biomass seaward. *Sargassum* sp. is the principal constituent; *Dictyota* sp., *Lobophora* sp., and *Stylopodium* sp. are abundant; and *Galaxaura* sp. and *Neomeris* sp. are common. Veneers of turf-stabilized sediment combine with red boring algae to form the predominant cover. Sand channels that are common in the shallow, inner fore-reef pavement decrease along the outer part of the transect. Mounds of coral are present on the pavement adjacent to the edges of channels and holes. Corals associated with the mounds are *Diploria strigosa*, *Siderastrea radians*, *S. siderea*, *Montastrea annularis*, and *Agaricia agaricites*. Corals, large octocorals, and vase-shaped and encrusting sponges are found on the outer pavement, but they are sparse.

**QUEEN CAY, SOUTHERN PROVINCE** (Figure 223g).—This transect crosses a 1.2 km section of reef, the longest segment of shallow-water reef south of Gladden Spit (Figure 222). Typical of

southern province reefs that form reentrants, the back-reef flats are generally much narrower and the lagoons deeper than in the north. From the lagoon, a moderate slope ascends into coral mounds surrounded by scattered rubble. Patches of seagrasses occur in some of the slightly deeper water on the back-reef flat. Mounds of corals and coralline algae increase in size and frequency as they grade into the reef crest. Surface cover on mounds is primarily turf and encrusting coralline algae, but coral cover can reach 15 percent. Rubble is not prominent except in the crest, where it covers the moderately deep ( $\approx$ 1 m) grooves between the broad massive spurs. These spurs coalesce locally to form the irregular reef crest. Turf, encrusting coralline algae, and *Sargassum* sp. are predominant, with lesser amounts of *Palythoa* sp. and *Millepora complanata* also present. *Turbinaria turbinata* occurs on the shallowest mound surfaces. Thickets of *Acropora palmata*, covering 50–60 percent of the bottom, occur immediately seaward of the reef crest and locally interfinger with the crest where mounds are spaced more widely. The low-relief spur and groove zone is mainly a turf-covered pavement with coral coverage approaching 25 percent. In places, the bottom is as much as 60 percent coarse sand; the remainder consists of low, turf-covered spurs. *Gorgonia* sp. and other octocorals mark the deeper parts of the spurs, spanning the transition from spurs to fleshy algal pavement. Spurs grade abruptly into a broad pavement where the most conspicuous components are *Sargassum* sp. and *Dictyota* sp. Encrusting and vase-shaped sponges highlight the surface.

Near the shelf edge, a spur and groove zone with moderate relief is formed, and coral diversity and population densities increase. Dominant corals are listed in Figure 223g. Some of the less conspicuous forms include *Madracis asperula*, *Eusimila fastigiata*, *Stephanocoenia michelinii* Milne Edwards and Haime, *Meandrina meandrites*, *Dichocoenia stokesi*, *Mycetophyllia* spp., and *Porites porites*. *Acropora cervicornis* is found only along margins in the upper parts of grooves along the shelf edge. *Lobophora* sp. becomes increasingly abundant across the shelf-edge spur and groove zone. The

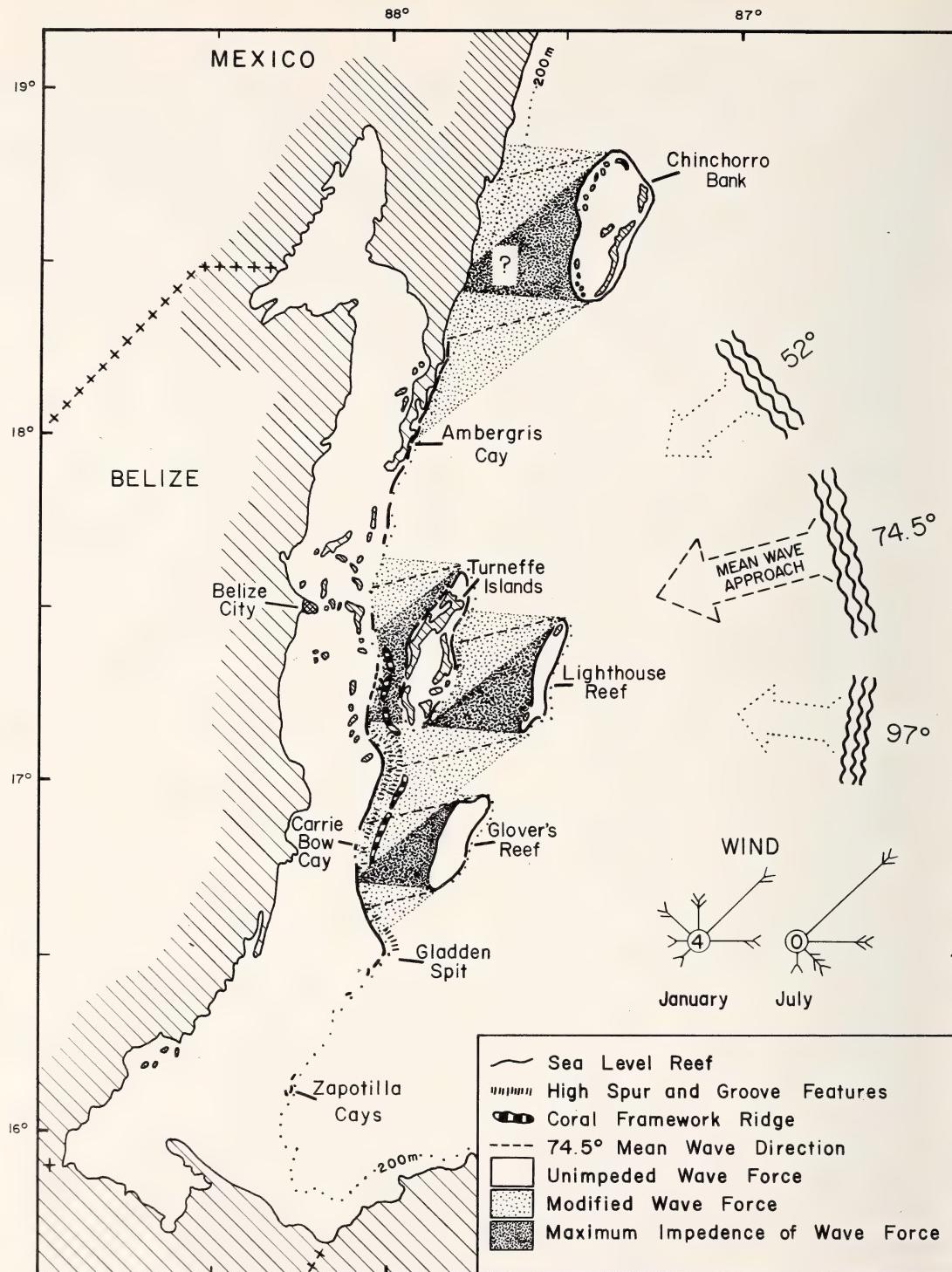


FIGURE 224.—Simplified diagram of the relationship between the magnitude of wave energy and sea level reefs, spur and groove features, and shelf-edge ridges along the Belizean barrier reef. Wave force impact on the reefs is controlled by wind speed and direction and by the impedance and modifying effect of the off-shore carbonate platforms. Wave patterns indicate mean wave direction ( $74.5^\circ$ ) and plus and minus  $22.5^\circ$  ( $97^\circ$  and  $52^\circ$ ), the sector containing 87% of the frequencies. Note the extensive development of fore-reef structures in the shaded (wave impeded) zones. The question mark indicates lack of data for the shelf edge behind Chinchorro Bank.

fore-reef slope along the shelf edge drops abruptly from 27 m to below 1400 m.

### Discussion and Conclusions

The Belizean barrier platform has a reef built within 0.2 m of sea level along 57 percent of its length. Of this sea level reef development, approximately 31 percent occurs in the northern province, 62 percent in the central province, and 6 percent in the southern province. The distribution of fore-reef structures, their associated communities, and the distribution of the shallow-water reef system correlates with the distribution of wave energy reaching the barrier reef (Figure 224). Mean wind direction, and thus mean wave direction, is equal to  $74.5^\circ$  (east-northeast) as determined by vector addition of directional frequencies of the wind. More than 95 percent of the waves along the fore reef come from easterly directions between  $0^\circ$  (north) and  $180^\circ$  (south). The remaining 5 percent are from westerly directions, particularly the northwest, and have little mechanical effect on the fore-reef communities. Eighty-seven percent of the easterly waves come from between  $52^\circ$  and  $97^\circ$ , or  $45^\circ$  about the mean wind. Wave energy impinging on the barrier reef is differentially attenuated and modified by the three carbonate platforms lying seaward of the barrier reef (Turneffe Islands, Lighthouse Reef, and Glover's Reef). The amount of wave modification and decrease in wave force depends on the direction of the incoming wave train relative to these carbonate platforms.

The shelf-edge coral ridge and the shallow, high-relief spur and groove systems occur only in the zone of modified wave force. Preliminary calculations of mean annual wave energy indicate that the coral ridge occurs where wave energy is reduced to less than 40 percent of the total unimpeded wave energy. Shallow fore-reef spur and groove structures of high relief occur where wave energy is between 25 to 50 percent of the total.

Double high spur and groove formations occur where wave energy is between 40 and 50 percent of the total. The positive correlation between zones of impeded and modified wave forces and extensive shallow-water reefs with abundant fragile corals in the fore reef suggests that seaward platforms have affected favorably the development of a continuous barrier reef in the central province by interfering with regional wave energy. Where open ocean waves have full access to the barrier reef, durable, slow-growing communities prevail and shallow-water reefs are narrow and discontinuous.

High-relief spurs and coral ridges built by fragile branching corals are uncommon in Caribbean reefs. From the literature and personal observation of over 80 percent of the windward Caribbean coastlines, similar community development and structures are known only from Jamaica, north Haiti, and southeast Alacran. All of these areas are exposed to modified wave settings and are protected from long-period storm waves generated by prolonged and severe mid-latitude winter storms. Exposure to such severe wave energy conditions was postulated to account for the absence of emergent shelf-edge reefs in the eastern Caribbean (Adey, 1978). Conversely, protection from such extreme conditions has affected significantly the shelf-edge development along the central province of Belize by encouraging high rates of carbonate production and accumulation by rapid-growing, branching corals (Adey, 1978; Burke, 1979).

Obviously, other factors have substantially influenced present reef distribution on the outer Belizean platform. A model proposed by Adey and Burke (1977) incorporating wave energy, turbidity, and pre-Holocene shelf depth was applied by Burke (1979) to explain Holocene reef development and distribution along the platform. This subject will be presented in greater detail in a forthcoming paper by Burke.

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# Species-Area Relationships on Small Islands: Floristic Data from Belizean Sand Cays

David R. Stoddart  
and F. Raymond Fosberg

## ABSTRACT

Analysis of species records of plants from 34 sand cays on the barrier reef and atolls of Belize, Central America, shows a linear relationship between species number and the logarithm of island area over the range 0.13 ha to 16.50 ha. Shrubs and trees show only a slight increase in numbers with area, because of the small number of shrubs available to colonize available habitats and the clearing of native woodland for coconut plantations. Herb numbers increase more strongly with island area, probably as a result of disturbance of habitats by man. Distance from source areas forms a much weaker control of species numbers, because of the proximity of the cays to Central America and their equal distance from eastern Caribbean source areas. Comparison with other island groups, however, shows that the Belize cays have much larger floras than more remote oceanic islands of similar sizes. Limited inferences on colonization and extinction can be made from the species records.

## Introduction

This paper presents the results of floristic studies on sand cays of the barrier reef and lagoon and the three offshore atolls (Turneffe Islands, Glover's Reef, Lighthouse Reef) of the coast of Belize (formerly British Honduras), Central America (Figure 225).

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Niering's (1963) study of the distribution of vascular plants on islets of Kapingamarangi Atoll, eastern Caroline Islands, showed constant species numbers independent of island size below a threshold of 1.4 ha, and a linear relationship between species number and logarithm of island area above this threshold (Figure 226). Wiens (1962:369) suggested that the threshold marked the size of the smallest island supporting a fresh-water lens under Kapingamarangi rainfall conditions (mean annual rainfall 2000 mm). These data, based on 31 islands ranging in size from 0.16 to 32.00 ha, were used by MacArthur and Wilson (1967) both to illustrate the fundamental control of species diversity by area, and also to suggest that on very small islands this control is less effective. Instead of Wiens' explanation, they proposed that very small islets are regularly subject to inundation and wave damage during storms, and that below a threshold of island stability, periodic extinction of species could be complete. Supporting data used by MacArthur and Wilson came from earlier surveys of the Dry Tortugas and the Florida Keys (Millspaugh, 1907; Bowman, 1918), though recent work has shown that the Dry Tortugas data are unreliable (Stoddart and Fosberg, in prep.).

The Kapingamarangi data provided an apparently simple illustration of MacArthur and Wilson's equilibrium theory of island biogeography: on the local (within-atoll) scale, area is the main determinant of species number, whereas the species pool available for colonization of the islands is filtered on a regional scale by distance from

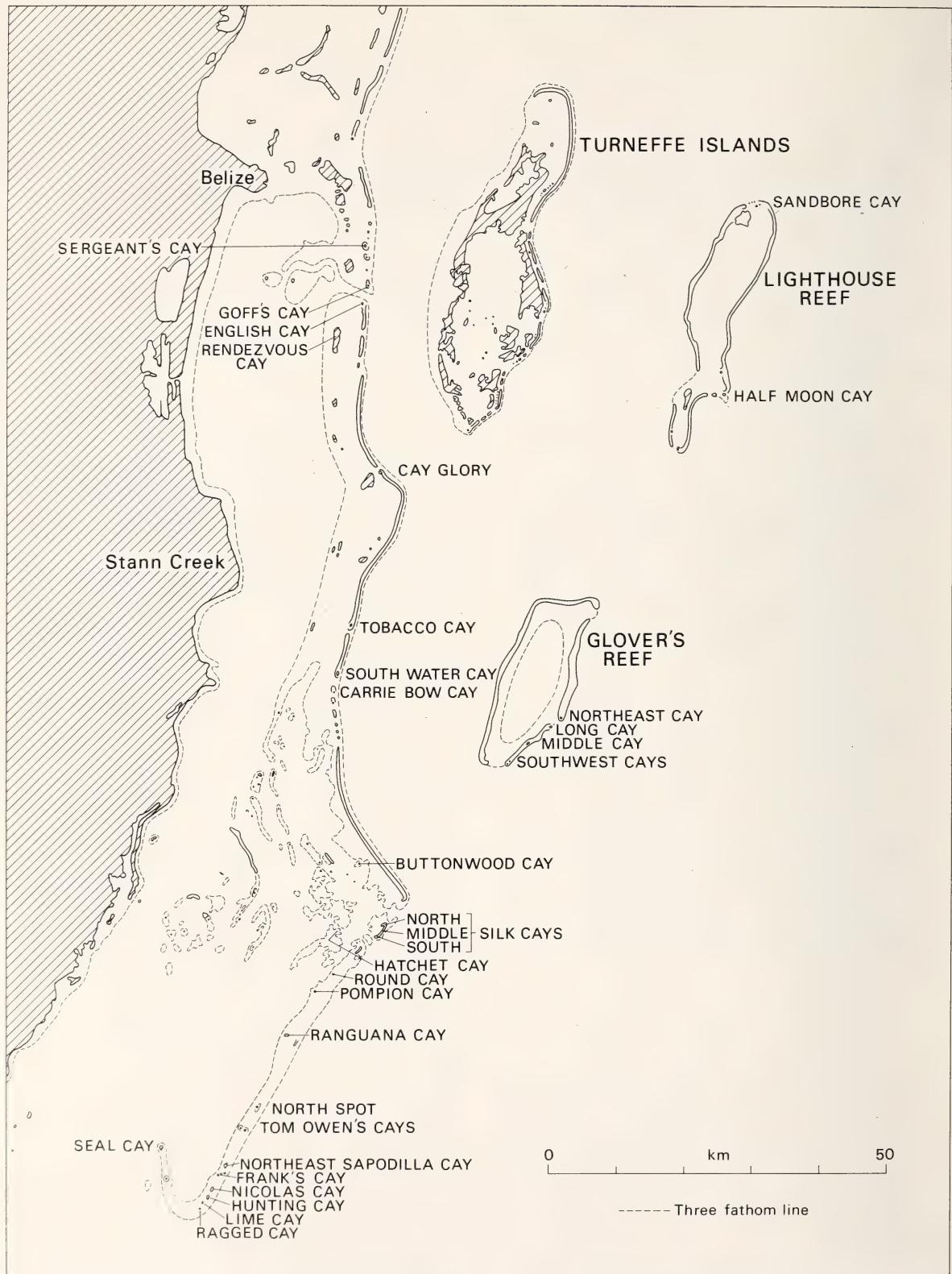


FIGURE 225.—Reef islands of the Belizean coast.

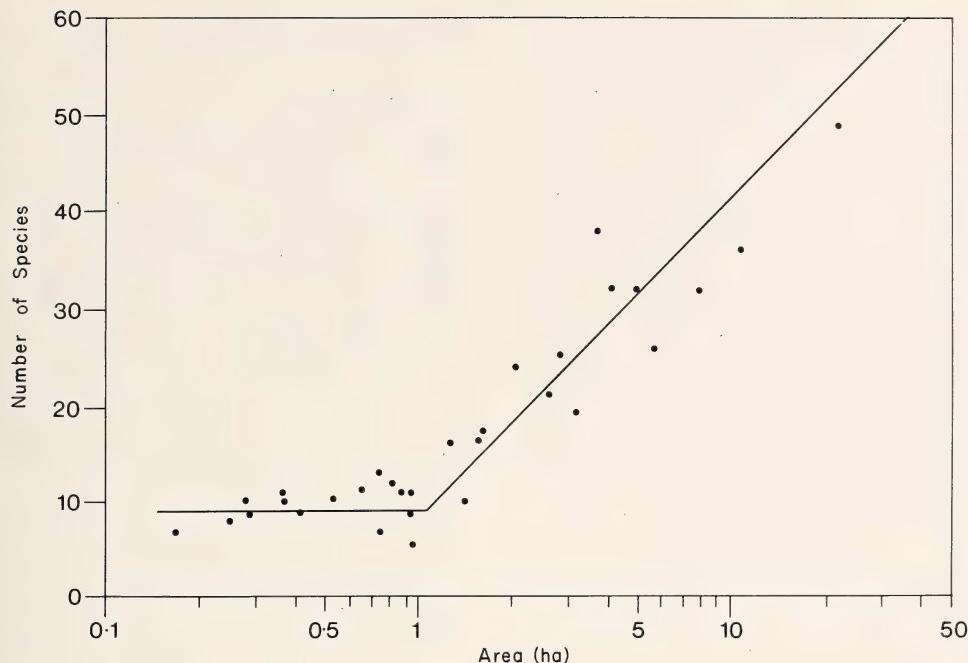


FIGURE 226.—Relationship of number of species to logarithm of island area for plants on Kapingamarangi islands (source: Niering 1963:137).

continental sources. Niering's analysis was further refined by Whitehead and Jones (1969), who classified the species on each of the Kapingamarangi islands into ecological groups: strand (salt-tolerant) species; non-strand species; and introduced species. They showed that the smallest islands on Kapingamarangi supported only strand species, and that introduced species were most numerous on larger, inhabited islands. Numbers of strand species per island were only weakly influenced by area, presumably because the pool of such species is itself limited in size, whereas the number of non-strand species increased sharply with increasing area. Whitehead and Jones (1969:176) concluded that "species diversity on both the large and small islets is controlled primarily by the ecology of the island." Unfortunately they did not indicate which species in the total flora of 99 species they assigned to each ecological category; the status of many must necessarily be conjectural.

A rather different analysis of the same data was made by Stoddart (1975), who grouped the species into categories of herbs, shrubs, and trees.

It was shown that (a) numbers of shrub species did not vary greatly with area because of the limited number of such species present in the Western Pacific and capable of surviving on such islands; (b) numbers of tree species did not increase on larger islands, largely because indigenous forests had been replaced by coconut plantations; and (c) herb species numbers (which include many weedy species) increased dramatically on larger, inhabited islands as a result of human interference with natural vegetation. Similar results came from an analysis of data from Aitutaki, Cook Islands, for 15 islands ranging in size from 1.0 to 71.3 ha. The Aitutaki case is particularly interesting, for the total flora is small (53 species) even though the islands are immediately adjacent to an inhabited volcanic island which forms a local reservoir of possible colonizers. The fact that many species have failed to colonize across a water gap of less than 10 km suggested that the restricted flora on the islets reflected ecological control rather than the remoteness of Aitutaki itself from source areas. There remains, however, a dearth of floristic data

on similar small islets with which the interpretations of MacArthur and Wilson (1967) and Whitehead and Jones (1969) can be tested and refined.

**ACKNOWLEDGMENTS.**—This paper results from collections made by Stoddart during 1959–1965, supported by the Department of Scientific and Industrial Research (London), the Office of Naval Research (Washington), the Coastal Studies Institute (Louisiana State University), and the Royal Society (London); by Fosberg, M.-H. Sachet (Smithsonian Institution), and Stoddart on Glover's Reef in 1971, as part of the Smithsonian Institution's CITRE (Comparative Investigations of Tropical Reef Ecosystems) Program; and by Fosberg, D. L. Spellman (Missouri Botanical Garden), and Stoddart along the barrier reef in 1972, as part of the Smithsonian Institution's IMSWE (Investigations of Marine Shallow-Water Ecosystems) Program.

### Methods and Data

Sand cays have been mapped on the coast of Belize in 1960, 1961, 1962, 1965, 1971, and 1972, all more than once and many on several occasions, and vascular plants have been both collected and recorded. The islands are accumulations of coral cobbles and reef-derived sand, mostly 50 to 200 m in greatest dimension, exceptionally reaching 1500 m, usually rising 1 to 3 m above mean sea level and occasionally reaching 5 m. They support a varied vegetation of pioneer herbs, vines and grasses, scrub, scrub woodland, broadleaf forest, and coconut woodland, with, in protected situations, mangrove woodland. All the islands are periodically subject to severe hurricane damage. Island areas reported here derive from planimetric measurements of maps made during the surveys. Where the areas have changed over the period of study, the figure quoted is that for the most recent survey, usually 1971 or 1972 (Stoddart, 1962, 1963, 1965, 1974).

The total cay flora comprises approximately 171 species, of which 68 are common to islets of the coastal barrier-lagoon system and to one or more of the atolls, 91 are found only on the

barrier and or lagoon cays, and 12 are restricted to the atolls. One hundred and fifty eight species are found on the barrier and lagoon islets, of which 31 are introduced. The three offshore atolls have a combined flora of 87 species (of which three are introduced): 36 are recorded from Turneffe, 55 from Lighthouse Reef, and 63 from Glover's Reef. The atoll records, which reflect collecting intensity, compare with other Caribbean atolls as follows: Dry Tortugas, 45 species, plus more than 50 introductions (Millspaugh, 1907; Bowman, 1918; Davis, 1942); Alacran, 25 species, including 5 introductions (Fosberg, 1962), Morant Cays, 16 species, including one introduction (Chapman, 1944; Asprey and Robbins, 1953), and Pedro Bank, 10 species, including one (possibly two) introductions (Zans, 1958; Fosberg, unpublished records in 1962; Chapman, 1944).

Plants have been recorded from a total of 97 Belizean reef islands. The records suggest that the floristic data are sufficiently comprehensive for analysis for 40 islands, but other considerations (such as presence of extensive mangroves) reduced this to 34, located as indicated in Tables 44 and 45. The most extensive plant collecting was carried out by Fosberg, M.-H. Sachet, and Stoddart on Glover's Reef in 1971, and by Fosberg, D. L. Spellman, and Stoddart on the barrier reef and lagoon cays in 1972, supplementing earlier collections made by Stoddart in 1960, 1961, 1962, and 1965. The vegetated islands studied range in size from 0.13 ha (North Spot) to 16.5 ha (Half Moon Cay); islands smaller than 0.10 ha did not possess vascular plants (for instance, Curlew Cay, 0.03 ha; Paunch Cay, 0.06 ha). Most of the collections made are represented in the U.S. National Her-

TABLE 44.—Number and location of Belizean reef islands for which data on vegetation are available

Location	Data available	Data acceptable	Data used
Barrier reef	29	25	24
Lagoon	34	5	2
Turneffe Islands	22	0	0
Lighthouse Reef	6	4	2
Glover's Reef	6	6	6

barium, with a fairly good set at the Missouri Botanical Garden.

## Results

**SPECIES-AREA-DISTANCE RELATIONSHIP.**—Numbers of species of vascular plants, excluding seagrasses, for the 34 selected islands are plotted against logarithmic island area in Figure 227, and the data are listed in Table 45. As in Amerson's (1975) study of the Leeward Hawaiian Islands, species number refers to the total number of species ever recorded from the island rather than the number recorded during a single survey. Under conditions of rapid turnover, therefore, it will generally exceed the number of species present at any one time. Twenty of the islands are smaller than Wiens' Kapingamarangi threshold of 1.4 ha, but no inflection is apparent in the Belize distribution; there is a linear relationship between species number and logarithm of island area over the range 0.13 ha to 16.5 ha.

The species recorded for each island have also been classified into trees, shrubs, and herbs, and each category plotted against logarithmic area in Figure 228. Assigning species to these categories

raises considerable problems. Decisions have been made on a taxonomic rather than a physiognomic basis, so that a tree species is recognized even if only a seedling is present. Some distinctions are arbitrary; thus, all mangroves are classified as trees except for *Conocarpus erecta* Linnaeus, which is classified as a shrub. Assignments are consistent between islands, in spite of considerable differences in size and habit of individual plants in different places.

Shrubs and trees show a very slight increase in numbers with area, because of the restricted size of the shrub species pool capable of colonizing such small islands; because some shrub species (notably *Suriana maritima* Linnaeus) may form extensive single-species stands on larger islands, thus excluding other shrub species; and because most of the islands now support coconut woodland rather than indigenous forest. Herb numbers increase more dramatically with area, probably as a result of the prevalence of weedy species and human introductions on larger islands, especially those that are inhabited, and by the provision of suitable habitat for these species on periodically cleared ground under coconuts. Abnormally low herb numbers on some larger islands can be

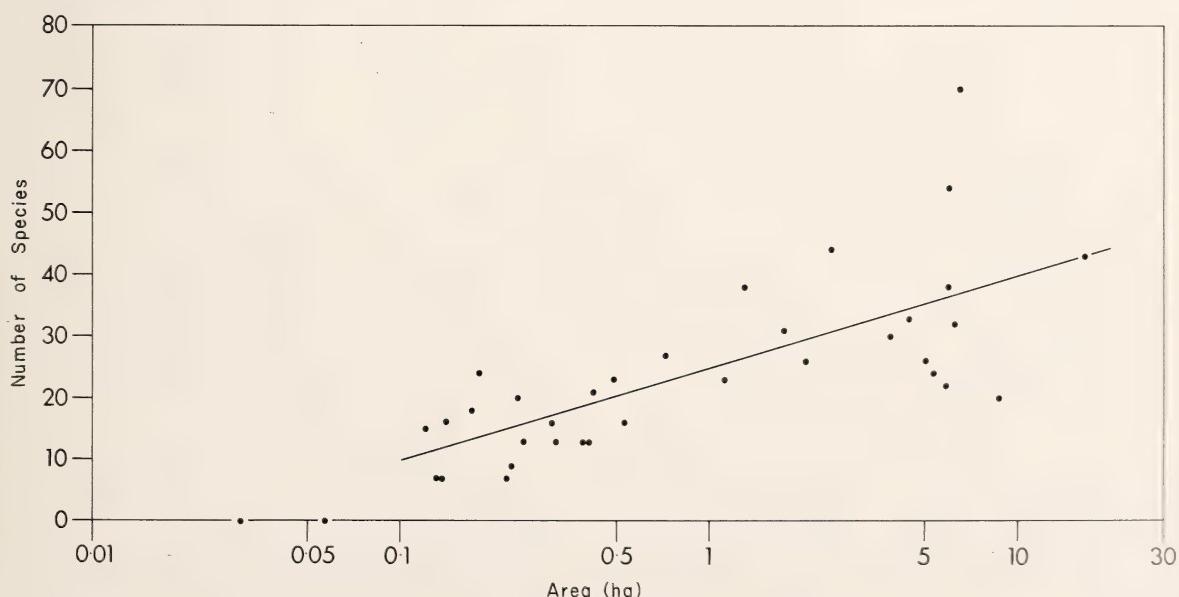


FIGURE 227.—Relationship of number of species to logarithm of island area for plants on Belizean reef islands.

TABLE 45.—Records of vascular plants from Belizean reef islands (listed north to south within each geographic feature)

<i>Island</i>	<i>Total number of species</i>	<i>Number of tree species</i>	<i>Number of shrub species</i>	<i>Number of herb species</i>	<i>Area (ha)</i>	<i>Distance from mainland (km)</i>
<b>BARRIER REEF</b>						
Sergeant's	20	4	3	13	0.17	18.7
Goff's	13	3	0	10	0.32	25.7
English	23	5	2	16	0.49	24.4
Rendezvous	24	6	3	15	0.18	26.4
Cay Glory	7	1	0	6	0.13	25.7
Tobacco	44	9	7	28	2.50	18.2
South Water	70	11	9	50	6.49	18.4
Carrie Bow	13	3	1	9	0.39	18.7
North Silk	13	3	4	6	0.25	36.0
Middle Silk	13	1	4	8	0.40	36.0
South Silk	9	2	1	6	0.23	36.0
Round	16	3	3	10	0.31	32.6
Pompion	21	7	4	10	0.42	31.3
Ranguana	23	3	3	17	1.12	32.6
North Spot	7	2	1	4	0.13	34.1
Tom Owen's West	20	4	2	14	0.24	33.3
Tom Owen's East	15	3	3	9	0.12	33.6
Northeast Sapodilla	26	6	4	16	5.06	36.0
Frank's	31	7	4	20	1.74	35.5
Nicolas	30	7	6	17	3.86	35.7
Hunting	54	13	8	33	5.94	36.2
Lime	26	5	3	18	2.07	36.2
Ragged	7	2	1	4	0.22	35.5
Seal	16	7	1	8	0.14	27.8
<b>BARRIER LAGOON</b>						
Buttonwood	27	6	3	18	0.72	30.5
Hatchet	38	7	4	27	1.30	32.1
<b>LIGHTHOUSE REEF</b>						
Sandbore	24	4	5	15	5.34	73.6
Half Moon	43	10	6	27	16.50	78.3
<b>GLOVER'S REEF</b>						
Northeast	33	9	5	19	4.48	52.2
Long North	16	2	4	10	0.53	51.5
Long	22	5	5	12	5.85	51.0
Middle	38	11	5	22	5.97	49.5
Southwest I	20	4	3	13	8.70	49.5
Southwest II	32	3	3	26	6.23	45.5

explained either by the persistence of dense thicket instead of coconut woodland (as on Nicolas Cay), or by the presence of extensive marshy areas within the cay, which reduce its effective area for dry-land plants (as on Northeast Sapodilla Cay and Southwest I Cay). The results of this analysis thus resemble those carried out for

Aitutaki and Kapingamarangi (Stoddart 1975, fig. 33).

Floristic diversity has also been analyzed in terms both of island area and of distance from the mainland coast of Central America. Linear, quadratic, and cubic trend surfaces have been fitted to species number data on coordinates of

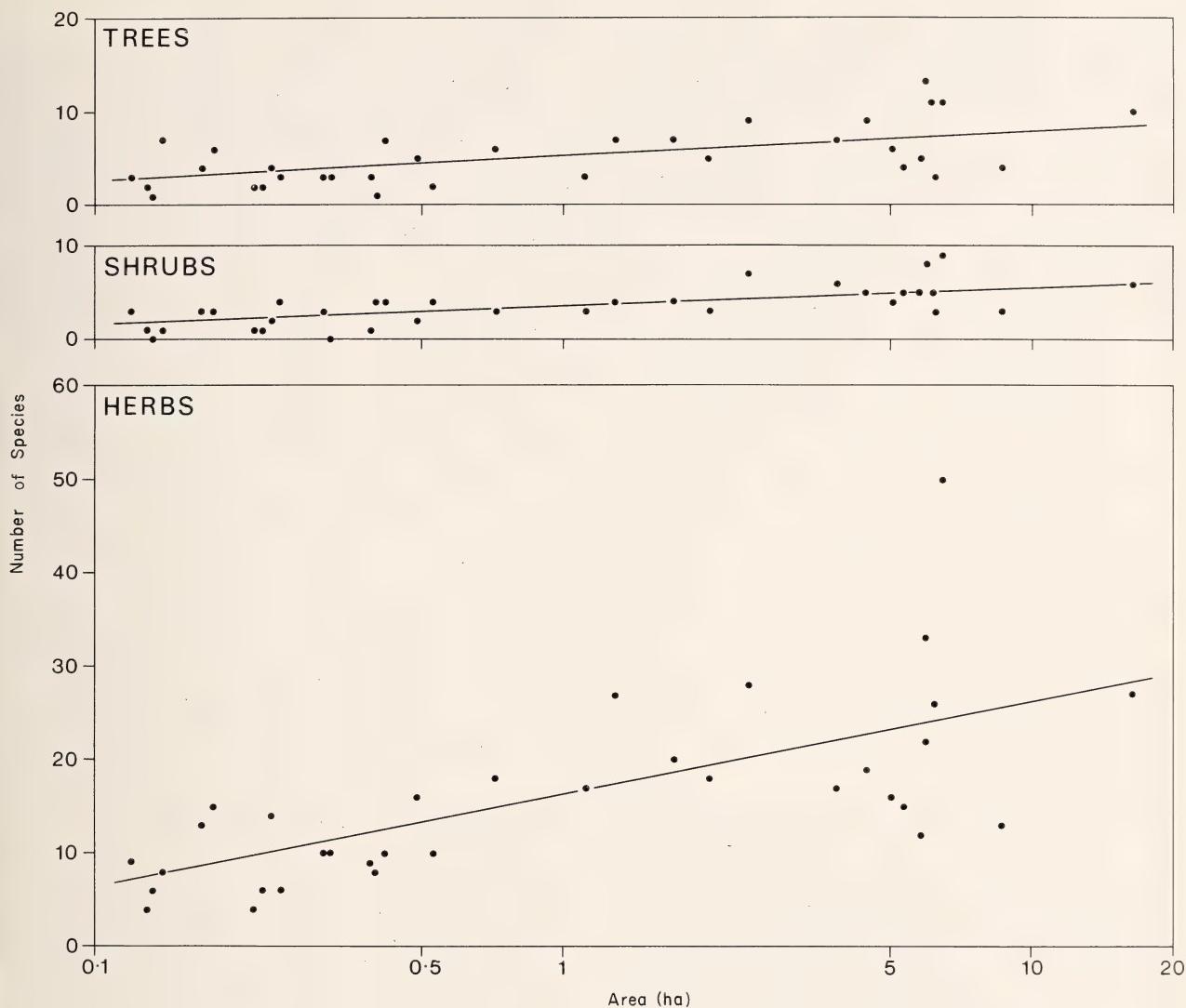


FIGURE 228.—Relationship of number of species to logarithm of island area for trees, shrubs, and herbs on Belizean reef islands.

logarithmic island area ( $\text{ha} \times 10$ ) and logarithmic distance from mainland (km). This has been done both for total species and for total less introduced species. Values of  $R^2$  for the surfaces are given in Table 46.

Equations for the linear surfaces are

$$z_1 = 75.17702 + 18.96162x - 45.58615y$$

$$z_2 = 56.09279 + 17.58632x - 33.31592y$$

where  $z_1$  is number of all species,  $z_2$  is number of indigenous species,  $x$  is logarithmic island area

( $\text{ha} \times 10$ ), and  $y$  is distance from mainland in km. Figure 229 plots the  $z_1$  surface for the islands studied and illustrates the relatively weak influence of distance compared with area, as might be expected for dominantly water-dispersed plants so close to continental shores.

The use of a parameter such as distance from mainland to indicate isolation is not particularly useful. Currents in the region are dominantly north-south, transverse to the shortest-distance paths between islands and mainland, and since the area is affected by the Northeast Trades, the mainland in fact is leeward of the cays. Distances

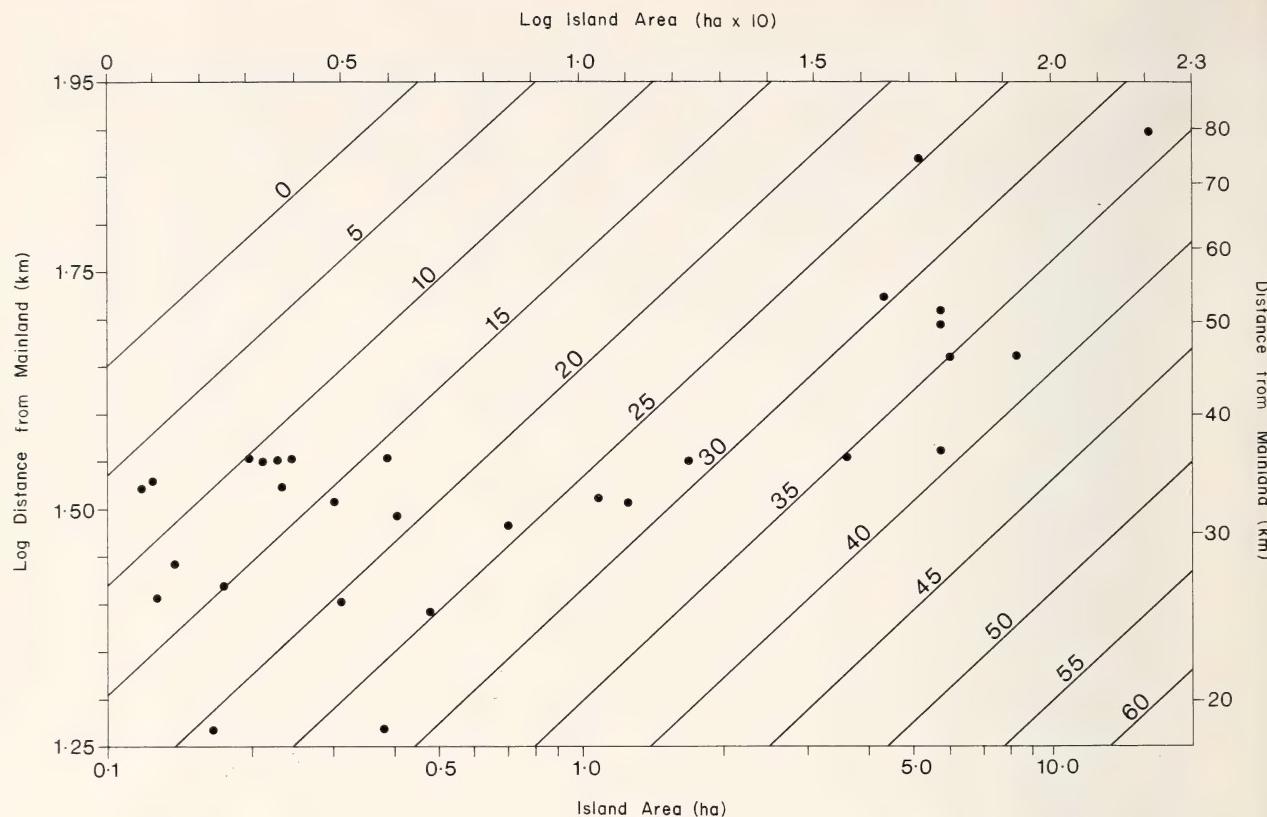


FIGURE 229.—Linear trend surface for total species number in terms of island area and distance from mainland for Belizean reef islands.

between the islands are probably insignificant for propagules arriving as drift from the eastern Caribbean. Circulation gyres in the Gulf of Honduras may also help to explain the remarkable absence on this coast of a species such as *Scaevola pulmieri* (Linnaeus) Vahl, which is widespread in the eastern Caribbean in similar habitats and which reaches the Cayman Islands (740 km to windward of Belize) and even the northern coast of Yucatan (Sauer, 1959, 1967) and the Nicaraguan reefs (Milliman, 1969:9). Nevertheless, the data pre-

sented in Figure 229 correspond with MacArthur and Wilson's prediction that highest species numbers will be found on large, near-to-mainland islands and lowest numbers on small, far islands, though this correspondence does not necessarily imply the operation of the mechanisms leading to dynamic equilibrium that they propose.

The effect of distance is more dramatically shown in the comparison of species numbers between one of the atolls (Glover's Reef), Alacran Reef in the Gulf of Mexico, and Pedro Cays south of Jamaica (Figure 230). The higher diversities on Glover's Reef islands probably result from their proximity to the mainland, compared with the other more isolated reefs, although climatic differences may also be significant. Comparable rainfall records are not available for the three locations, but both Alacran and Pedro, with probably 1000 mm/y or less, are considerably drier

TABLE 46.—Plant diversity related to island area and distance of island from mainland coast

Trend surface	All species	Indigenous species
Linear	0.591	0.697
Quadratic	0.651	0.742
Cubic	0.681	0.779

than Glover's Reef. A similar inference may be drawn from Figure 231, which plots generalized curves for species numbers on the Belizean barrier islands, those of Kapingamarangi (Niering, 1963), and the leeward Hawaiian Islands in the central north Pacific (Amerson, 1975): the curves are of

similar form, reflecting the influence of area within each island group, but are displaced in magnitude, reflecting the effect of distance relative to source areas.

**SPECIES COMPOSITION CHANGES OVER TIME.**—Species turnover is more readily determined for

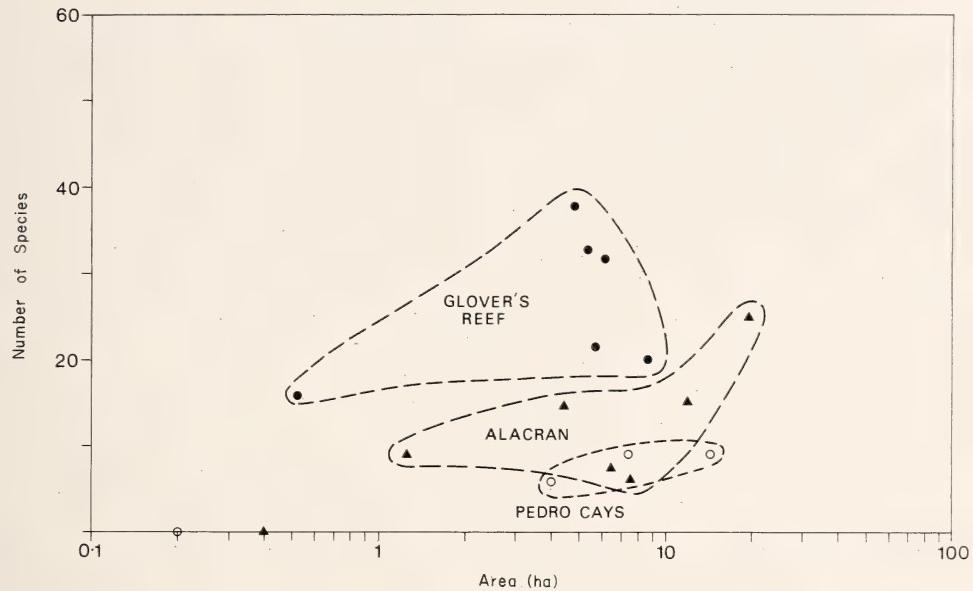


FIGURE 230.—Relationship of number of species to logarithm of island area for plants on individual islands on Glover's Reef, Alacran Reef, and Pedro Bank.

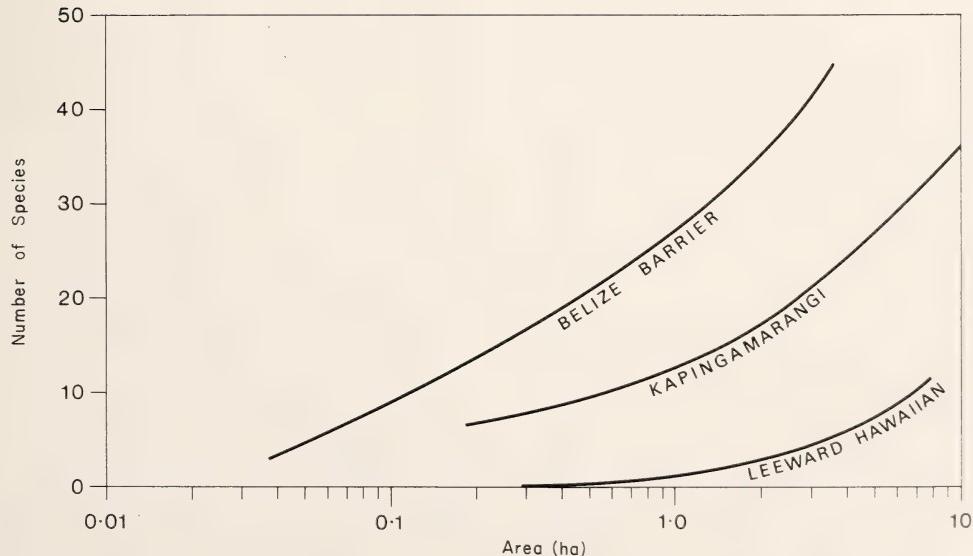


FIGURE 231.—Generalized species-area relationships for islands of the Belizean barrier reef, Kapingamarangi Atoll, and the Leeward Hawaiian Islands.

plants than for some other kinds of organisms (compare the criteria for avifaunal turnover discussed by Lynch and Johnson, 1974), but the problems of insuring completeness of the record are such that we do not think our data can support inferences of colonization or extinction from new records of plants made during repetitive surveys between 1960 and 1972. The single exception refers to small islands devastated by a major hurricane in 1961, where it has been possible to follow the course of plant colonization and re-vegetation (Stoddart, 1974). Data in Table 47 refer to four small islands on the northern barrier reef, the first three of which had their pre-existing plant cover entirely or almost entirely removed by the storm; the fourth retained a number of species, although all were much damaged. These data suggest that at least a decade is required for a small island to be re-stocked, and it would be useful to monitor the future development of these floras (compare also Rützler and Ferraris, herein: 77).

It is easier to infer local extinction from failure to find plants recorded during earlier surveys than it is to infer colonization. Extinctions are of two kinds: catastrophic extinction resulting from severe storm effects, of the kind envisaged by MacArthur and Wilson (1967) for the smaller Dry Tortugas; and local random extinction. In the case of beach-crest shrubs, the latter may result from small-scale beach retreat destroying a particular habitat to which a species is confined. This has occurred in the extinction of *Sophora tomentosa* Linnaeus on Tobacco Cay between 1965 and 1972, and of *Tournefortia gnaphalodes* (Lin-

naeus) R. Brown on Nicolas, Hunting, and Lime cays between 1960 and 1972. Extinctions of the first type occur only on smaller islands, generally smaller than 1 ha, but those of the second may be independent of island size. Since total species number is low on small islands, percentage turnover resulting from catastrophic damage is correspondingly high. Figure 232 plots extinctions on barrier reef islands determined in 1972 by comparison with records from 1960, 1962, and 1965, both as absolute numbers of extinct species against logarithmic area, and as percentages of the total number of species recorded from the island against logarithmic area. These data emphasize that very small islands (less than 0.5 ha) are particularly prone to extinction of their plants, as MacArthur and Wilson (1967:54–55) hypothesized.

### Discussion

The data reported here supplement those for Kapingamarangi and Aitutaki; they include data on many very small islands, over which controversy has centered; and they apply to islands with much higher species numbers than those previously discussed.

Total recorded species number varies directly with area over the whole size range of islands considered, down to 0.1 ha; there is no indication of the 1.4 ha threshold in area attributed by Wiens to the minimum size required for fresh-water lens formation, and by MacArthur and Wilson to the instability of substrates below this size. We have no records on fresh-water lens formation on Belizean islands (although fresh-water wells are not found on islands smaller than 2.5 ha). Our data suggest, however, that presence or absence of a lens may be less critical than Wiens supposed, especially in explanation of so crude a parameter as total species number and especially so far as herb species numbers are concerned. Further, hurricane activity on these islands is so regular and occasionally so intense that if a threshold of instability does exist, it may be higher than the 1.4 ha previously suggested. Nevertheless, there is no indication in the Beli-

TABLE 47.—Post-hurricane recovery of vegetation on four small barrier reef islands (data for each year include number of species and island area (ha) in parentheses)

<i>Island</i>	1962	1965	1972
Sergeant's Cay	4 (0.20)	12 (0.16)	14 (0.18)
Goff's Cay	2 (0.23)	4 (0.29)	10 (0.32)
English Cay	2 (0.34)	5 (0.35)	18 (0.49)
Rendezvous Cay	16 (0.22)	16 (0.20)	17 (0.18)

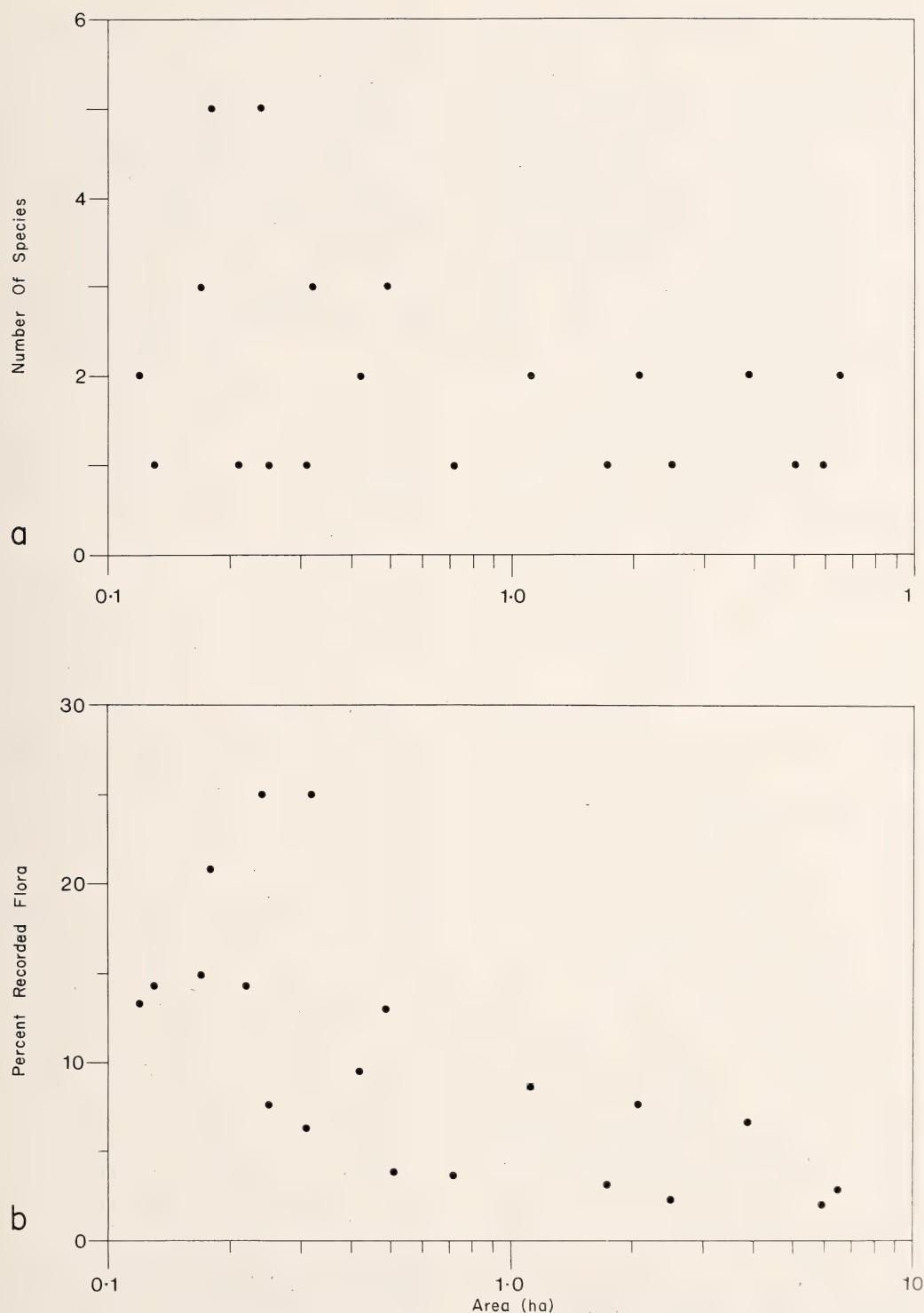


FIGURE 232.—Species extinctions on Belizean barrier reef islands between 1960 and 1972: *a*, absolute number of species extinct; *b*, extinctions as a percentage of the total recorded flora of the island.

zean data of any marked discontinuity in the area control.

The evidence also indicates that with the Belizean reef system, distance from mainland is a relatively weak control of species number on islands. Both Ridley (1930:689) and Carlquist (1974:45-96) have noted that many island species are water-dispersed with high efficiency, and that many are pan-tropical or at least extremely wide-ranging in their distribution. There is also negative evidence of the unimportance of distance as a diversity control in the absence of many species on coral islands, even when source reservoirs exist only a few kilometers away. This suggests that ecological controls are more important than location (Stoddart, 1975:93). Nevertheless, species-area curves for Belize, Alacran, Pedro Bank, Kapingamarangi, and the Leeward Hawaiian Islands, which vary widely in degree of isolation and also in floristic diversity, suggest that distance imposes a gross regional control by limiting numbers on the most distant islands.

The Belizean cays, however, lie close to continental shores, and we infer that their floras are not distance limited, as are those of the Leeward Hawaiian Islands. It follows that species numbers are not restricted by any reduction in the rate of propagule arrival, but rather by the ability of species to establish themselves once they have arrived, that is, by an ecological control. Although quantitative data are lacking, casual observation of germinating seeds indicates that a constant stream of propagules, many of which fail to develop into mature plants, is arriving on the islands. If it were not for this ecological control rendering many colonization attempts abortive, the floras of the islands could not be in equilibrium since known local extinction rates are probably low, except on the smallest hurricane-devastated islands.

This argument parallels that of Lack (1976:1-14) for West Indian birds. Lack documented many cases of the arrival of birds on islands where they failed to establish themselves (for example, hummingbirds on the Cayman Islands). He ascribed this phenomenon to ecological control

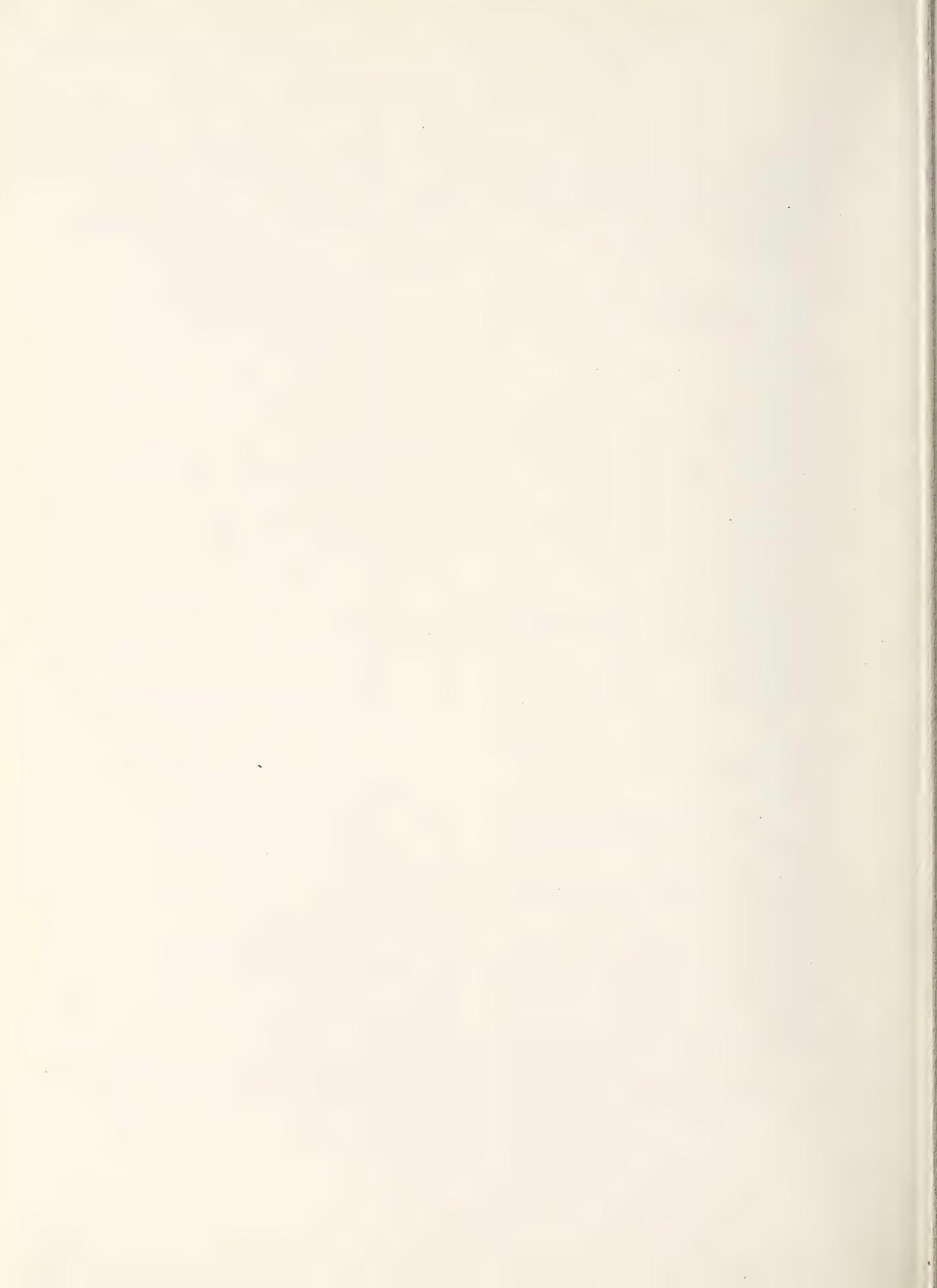
("ecological poverty"), while admitting that it was unclear how such control operated. We would like to draw attention to the need to study the mechanisms, notably environmental control and competition, which similarly prevent the establishment of plants. In contrast to the enormous literature on dispersal, which in our case is so effective as to be almost irrelevant in differentiating the floras of the cays, virtually no attention has been given to this crucial problem. Without such study, theoretical explanations of species numbers must remain speculative.

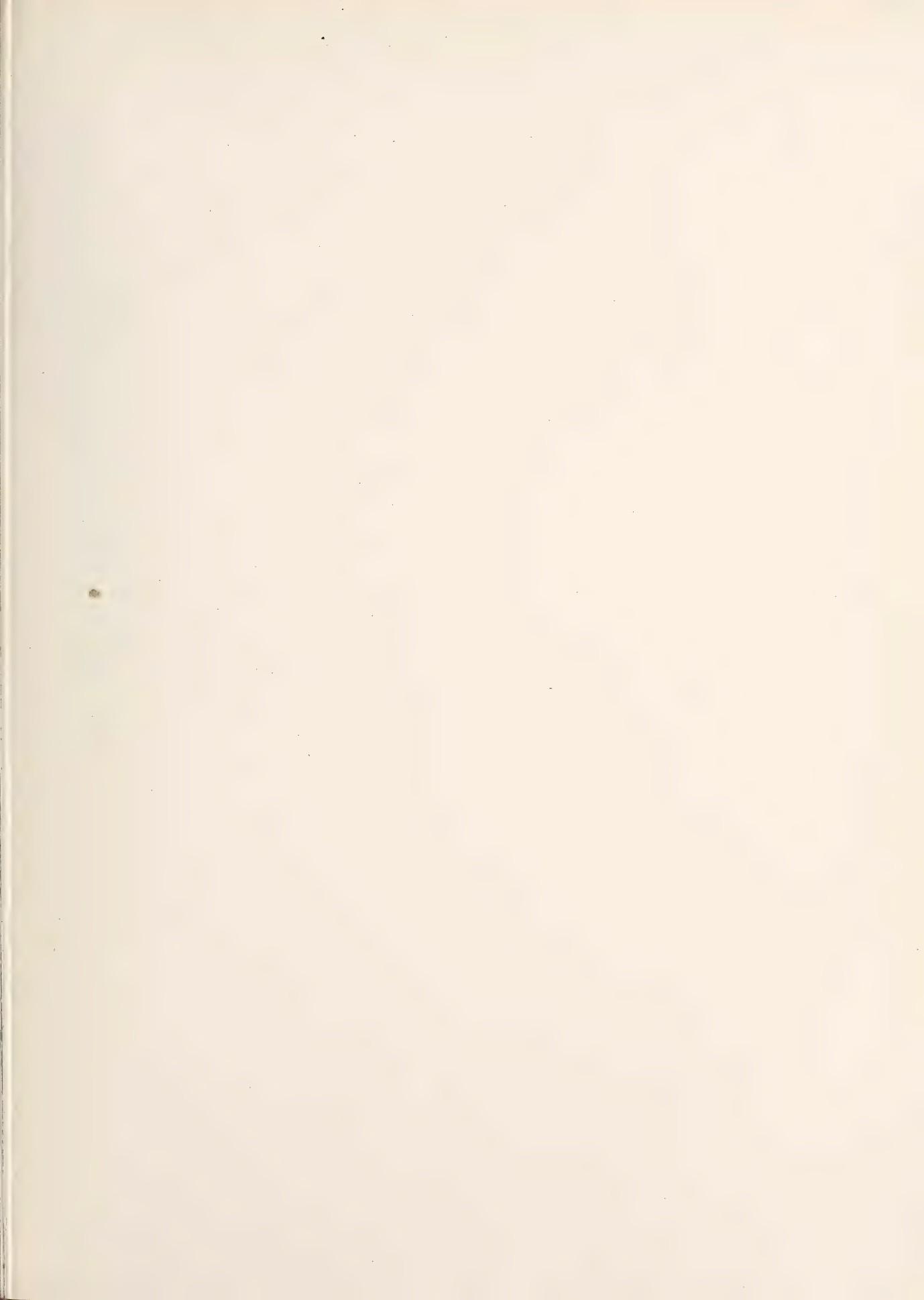
It is also possible that the closeness of the control of species numbers by area is much exaggerated by using aggregate numbers rather than numbers of species existing at any one time. Under conditions of high turnover, competition may lead to replacement of species rather than to packing of more species into a limited area, that is, the effects are temporal rather than spatial, so that species numbers remain constant at any time, but over time, the aggregate of species recorded increases up to a maximum set by the available species pool. The fact that many species often form extensive single-species stands on coral islands (for instance, *Scaevila taccada* (Gaertner) Roxburgh in the Indo-Pacific and *Suriana maritima* Linnaeus in the Gulf of Mexico) supports this suggestion. We have no means of estimating the effect of using aggregate species numbers in the Belizean case, but it may be noted that on Cayo Ahogado, Puerto Rico, admittedly an extremely small island (0.065 ha) with continuously changing topography, Heatwole and Levins (1973) recorded a total of 51 plant species; the maximum present at any one time was 21, and the number that might be considered established was only 9.

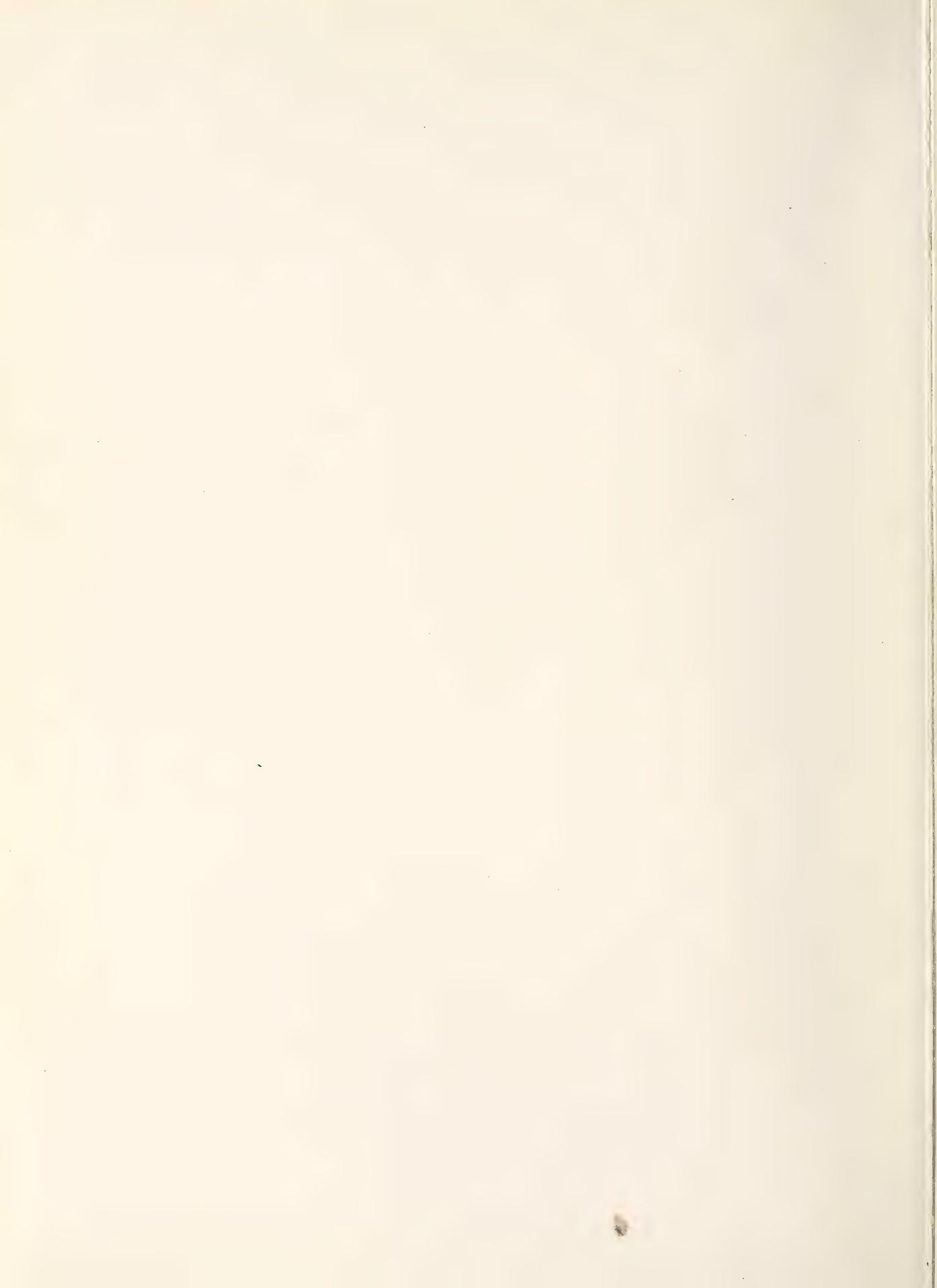
Finally, we would like to sound a note of caution. In spite of many years of activity by several workers on these islands, we would be reluctant to undertake a more sophisticated analysis, particularly of colonization and extinction, without a great deal more investigation. Our data will, however, serve as a basis for continued monitoring of floristic change on these islands in the future.

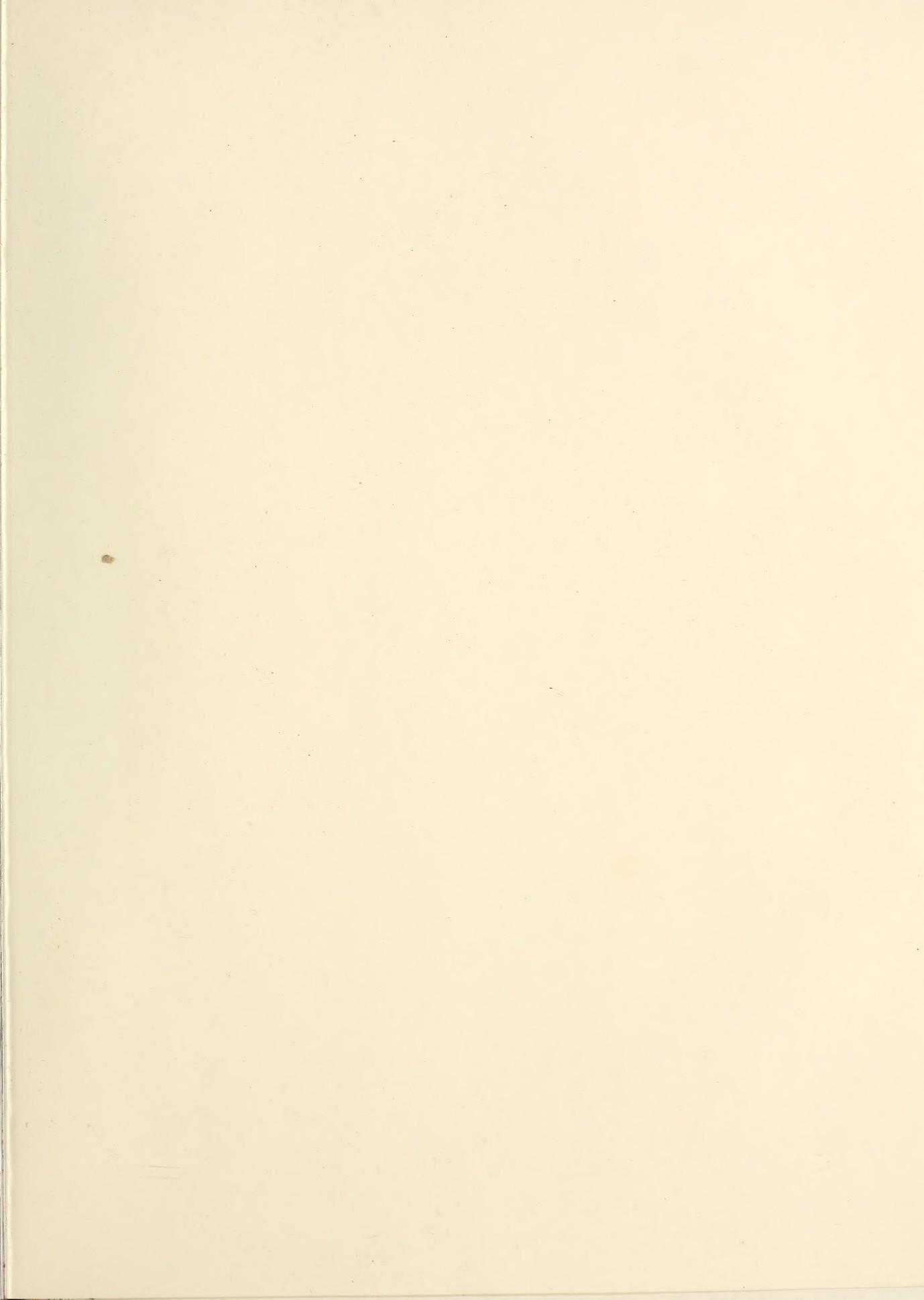
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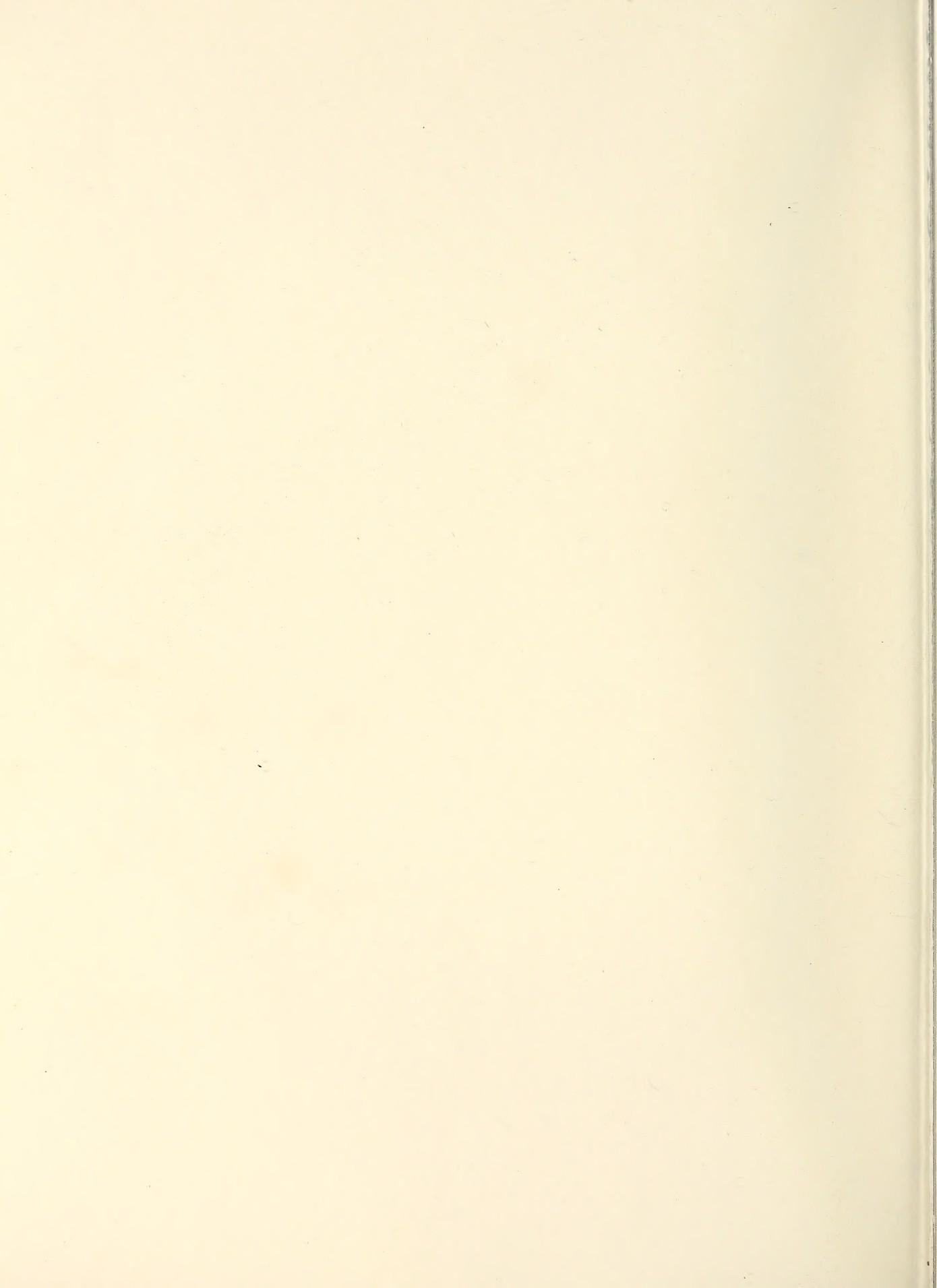
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